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VOLUME 84
1997

ALMEDA, FRANK. Chromosomal Observations on the Alzateaceae (Myrtales) 305

BACIGALUPO, NÉLIDA M. (See Elsa L. Cabral y Nélida M. Bacigalupo) 857

BENÍTEZ DE ROJAS, CARMEN & WILLIAM G. D'ARCY. The Genus *Lycianthes* (Solanaceae) in Venezuela 167

BERRY, PAUL E. Book Review. *Guide to the Vascular Plants of Central French Guiana. Part 1* by Scott Mori et al. 907

BLACKMORE, STEPHEN (See Sandra Knapp, Viveca Persson & Stephen Blackmore) 67

BROWN, K. D. (See J. F. Smith, J. C. Wolfram, K. D. Brown, C. L. Carroll & D. S. Denton) 50

CABRAL, ELSA L. Y NÉLIDA M BACIGALUPO. Revisión del Género *Galianthe* subg. *Ebelia* stat. nov. (Rubiaceae: Spermacoceae) 857

CARR, GERALD D. (See Harold Robinson, Gerald D. Carr, Robert M. King & A. Michael Powell) 893

CARROLL, C. L. (See J. F. Smith, J. C. Wolfram, K. D. Brown, C. L. Carroll & D. S. Denton) 50

CHASE, MARK W. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

CHAW SHU-MIAW (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

CROAT, THOMAS B. A Revision of *Philodendron* Subgenus *Philodendron* (Araceae) for Mexico and Central America 311

DENTON, D. S. (See J. F. Smith, J. C. Wolfram, K. D. Brown, C. L. Carroll & D. S. Denton) 50

D'ARCY, WILLIAM G. (See Carmen Benítez de Rojas & William G. D'Arcy) 167

D'ARCY, WILLIAM G. A Review of the Genus *Eccremocarpus* (Bignoniaceae) 103

FRITSCH, PETER W. A Revision of *Styrax* (Styracaceae) for Western Texas, Mexico, and Mesoamerica 705

GILLESPIE, LYNN J. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

GOLDBLATT, PETER & MASAHIRO TAKEI. Chromosome Cytology of Iridaceae—Patterns of Variation, Determination of Ancestral Base Numbers, and Modes of Karyotype Change 285

GOLDBLATT, PETER & ANNICK LE THOMAS. Palynology, Phylogenetic Reconstruction, and Classification of the Afro-Madagascan Genus *Aristea* (Iridaceae) 263

GU HONG-YA & PETER C. HOCH. Systematics of *Kalimeris* (Asteraceae: Astereae) 762

HAHN, WILLIAM J. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

HAUK, WARREN D. A Review of the Genus *Cydista* (Bignoniaceae) 815

HILU, KHIDIR, W. & JOHN L. JOHNSON. Systematics of *Eleusine* Gaertn. (Poaceae: Chloridoideae): Chloroplast DNA and Total Evidence 841

HOCH, PETER C. (See Gu Hong-ya & Peter C. Hoch) 762

HOOT, SARA B. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

JOHNSON, JOHN L. (See Khidir W. Hilu, & John L. Johnson) 841

JOHNSON, LEIGH A. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

KING, ROBERT M. (See Harold Robinson, Gerald D. Carr, Robert M. King & A. Michael Powell) 893

KNAPP, SANDRA, VIVECA PERSSON & STEPHEN BLACKMORE. A Phylogenetic Conspectus of the Tribe Juanulloeae (Solanaceae) 67

KRESS, W. JOHN (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

KRON, KATHLEEN A. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

KUZOFF, ROBERT K. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

LE THOMAS, ANNICK (See Peter Goldblatt & Annick Le Thomas) 263

LI JIE (See Li Xi-wen & Li Jie) 888

LI XI-WEN & LI JIE. The Tanaka-Kaiyong Line—An Important Floristic Line for the Study of the Flora of East Asia 888

MÉDAIL, FRÉDÉRIC & PIERRE QUÉZEL. Hot-Spots Analysis for Conservation of Plant Biodiversity in the Mediterranean Basin 112

NICKRENT, DANIEL L. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

PERSSON, VIVECA (See Sandra Knapp, Viveca Persson & Stephen Blackmore) 67

PIESSCHAERT, FREDERIC, ELMAR ROBBRECHT & ERIK SMETS. *Dialypetalanthus fuscescens* Kuhlm. (Dialypetalanthaceae): The Problematic Taxonomic Position of an Amazonian Endemic 201

PIRE, STELLA MARIS. Género *Galianthe* subg. *Ebelia* (Rubiaceae: Spermacoceae): Estudio Palinológico 878

POWELL, A. MICHAEL (See Harold Robinson, Gerald D. Carr, Robert M. King & A. Michael Powell) 893

QUÉZEL, PIERRE (See Frédéric Médail & Pierre Quézel) 112

ROBBRECHT, ELMAR (See Frederic Piesschaert, Elmar Robbrecht & Erik Smets) 201

ROBINSON, HAROLD, GERALD D. CARR, ROBERT M. KING & A. MICHAEL POWELL. Chromosome Numbers in Compositae, XVII: Senecioneae III 893

ROHWER, JENS G. The Fruits of *Jasminum mesnyi* (Oleaceae), and the Distinction Between *Jasminum* and *Menodora* 848

SCHUTTE, ANNE LISE. A Revision of the Genus *Xiphotheca* (Fabaceae) 90

SMETS, ERIK (See Frederic Piesschaert, Elmar Robbrecht & Erik Smets) 201

SMITH, J. F., J. C. WOLFRAM, K. D. BROWN, C. L. CARROLL & D. S. DENTON. Tribal Relationships in the Gesneriaceae: Evidence from DNA Sequences of the Chloroplast Gene *ndh*F 50

SOLTIS, DOUGLAS E., PAMELA S. SOLTIS, DANIEL L. NICKRENT, LEIGH A. JOHNSON, WILLIAM J. HAHN, SARA B. HOOT, JENNIFER A. SWEERE, ROBERT K. KUZOFF, KATHLEEN A. KRON, MARK W. CHASE, SUSAN M. SWENSEN, ELIZABETH A. ZIMMER, SHU-MIAW CHAW, LYNN J. GILLESPIE, W. JOHN KRESS & KENNETH J. SYTSMA. Angiosperm Phylogeny Inferred from 18S Ribosomal DNA Sequences 1

SOLTIS, PAMELA S. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

SWEERE, JENNIFER A. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

SWENSEN, SUSAN M. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

SYTSMA, KENNETH J. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

TAKEI, MASAHIRO (See Peter Goldblatt & Masahiro Takei) 285

TAYLOR, CHARLOTTE M. Conspectus of the Genus *Palicourea* (Rubiaceae: Psychotrieae) with the Description of Some New Species from Ecuador and Colombia 224

THOMPSON, MAXINE M. Survey of Chromosome Numbers in *Rubus* (Rosaceae: Rosoideae) 128

WOLFRAM, J. C., (See J. F. Smith, J. C. Wolfram, K. D. Brown, C. L. Carroll & D. S. Denton) 50

ZIMMER, ELIZABETH A. (See Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma) 1

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ANGIOSPERM PHYLOGENY INFERRED FROM 18S RIBOSOMAL DNA SEQUENCES[1]

Douglas E. Soltis,[2] *Pamela S. Soltis,*[2] *Daniel L. Nickrent,*[3] *Leigh A. Johnson,*[2] *William J. Hahn,*[4] *Sara B. Hoot,*[5] *Jennifer A. Sweere,*[4] *Robert K. Kuzoff,*[2] *Kathleen A. Kron,*[6] *Mark W. Chase,*[7] *Susan M. Swensen,*[8] *Elizabeth A. Zimmer,*[4] *Shu-Miaw Chaw,*[9] *Lynn J. Gillespie,*[10] *W. John Kress,*[11] *and Kenneth J. Sytsma*[12]

Abstract

Parsimony analyses were conducted for 223 species representing all major groups of angiosperms using entire 18S ribosomal DNA (rDNA) sequences. Although no search swapped to completion, the topologies recovered are highly concordant with those retrieved via broad analyses based on the chloroplast gene *rbc*L. The general congruence of 18S rDNA and *rbc*L topologies further clarifies the broad picture of angiosperm phylogeny. In all analyses, the first-branching angiosperms are Amborellaceae, Austrobaileyaceae, Illiciaceae, and Schisandraceae, all woody magnoliids. These taxa are always followed by the paleoherb family Nymphaeaceae. This same general order of early-branching taxa is preserved with several suites of outgroups. In most searches, the remaining early-branching taxa represent Piperales and other orders of subclass Magnoliidae (sensu Cronquist). With the exception of *Acorus*, the monocots are supported as monophyletic and typically have as their sister *Ceratophyllum*. In most analyses, taxa with uniaperturate pollen form a grade at the base of the angiosperms; a large eudicot clade is composed primarily of taxa having triaperturate pollen. Two large subclades are present within the eudicots, one consisting largely of Rosidae and a second corresponding closely to Asteridae sensu lato. Subclasses Dilleniidae and Hamamelidae are highly polyphyletic. These data sets of 18S rDNA sequences also permit an analysis of the patterns of molecular evolution of this gene. Problems deriving from both the prevalence of indels and uncertain alignment of 18S rDNA sequences have been overstated in previous studies. With the exception of a few well-defined regions, insertions and deletions are relatively uncommon in 18S rDNA; sequences are therefore easily aligned by eye across the angiosperms. Indeed, several indels in highly conserved regions appear to be phylogenetically informative. Initial analyses suggest that both stem and loop bases are important sources of phylogenetic information, although stem positions are prone to compensatory substitutions. Of the stem changes analyzed, only 27% destroy a base-pairing couplet; 73% maintain or restore base pairing.

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Although the angiosperms are almost universally considered to be monophyletic, many basic questions of angiosperm phylogeny remain unanswered, including: (1) what are the first-branching angiosperms? (2) what is the ancestor of the monocots? (3) what are the major groups of angiosperms and the relationships among these groups? Despite intensive study, these questions have been difficult to answer for a variety of reasons. Most notable, perhaps, is the inadequacy of the fossil record alone to answer these questions conclusively. In addition, the apparent rapid radiation of the angiosperms following their origin resulted in few morphological synapomorphies among lineages at the base of the angiosperm tree, hindering attempts to resolve relationships among major groups (Crane et al., 1995). Finally, the angiosperms present relatively few morphological characters for comparison at higher levels. For example, recent cladistic analyses of morphological characters for angiosperms (Donoghue & Doyle, 1989a, b) and all seed plants (Doyle et al., 1994) included only 54 and 82 characters, respectively. As recently demonstrated by Doyle et al. (1994), careful analysis of both morphological and molecular data is required to understand angiosperm phylogeny.

During the past decade, several attempts have been made to reconstruct the phylogeny of the angiosperms. Morphological and molecular analyses usually identify the Gnetales as the extant sister group to the angiosperms, in either the shortest trees or those slightly longer (e.g., Crane, 1985, 1988; Donoghue & Doyle, 1989a, b; Doyle & Donoghue, 1986, 1992; Loconte & Stevenson, 1991; Hamby & Zimmer, 1992; Chase et al., 1993; Doyle et al., 1994; Nixon et al., 1994; but see Goremykin et al., 1996; Chaw et al., 1997). Molecular phylogenetic analyses include those based on *rbc*L sequences (Chase et al., 1993), partial 18S and 26S ribosomal RNA sequences (Hamby & Zimmer, 1992), and *rbc*S amino acid sequences (Martin & Dowd, 1991). These analyses tend to identify many of the same major groups of taxa, but they often present different views of relationships among these groups.

In the largest phylogenetic analysis of angiosperms, Chase et al. (1993) presented the results of two parsimony analyses of DNA sequences from the chloroplast gene *rbc*L for 475 and 499 species of seed plants. More recently, Rice et al. (1997) have reanalyzed the 499-taxon *rbc*L data matrix to search for shorter trees. The benefits to the systematics community of performing these large phylogenetic analyses of seed plants in general, and angiosperms in particular, have been considerable. These studies provide comprehensive, explicit phylogenetic hypotheses of higher-level relationships in the angiosperms. Furthermore, the need for similar studies of angiosperms based on other character sets has been recognized, and such studies have been encouraged (e.g., Chase et al., 1993). Particularly important is the comparison of chloroplast-based phylogenetic estimates (Chase et al., 1993) with topologies derived from analyses of nuclear genes.

For reasons reviewed elsewhere, phylogenetic analyses based on nuclear DNA have largely involved portions of the rDNA cistron (e.g., Mindell & Honeycut, 1990; Hillis & Dixon, 1991; Hamby & Zimmer, 1992; Sanderson & Doyle, 1993a; Nickrent & Soltis, 1995). Analyses of 18S rDNA and rRNA sequences have been used for phylogenetic inference at higher taxonomic levels in animals (e.g., Sogin et al., 1986; Field et al., 1988; Wainright et al., 1993; Wada & Satoh, 1994), protozoa (Schlegel et al., 1991), algae (Buchheim et al., 1990; Huss & Sogin, 1990; Kantz et al., 1990; Hendricks et al., 1991; Chapman & Buchheim, 1991; Bakker et al., 1994; Ragan et al., 1994; Olsen et al., 1994), fungi (Forster et al., 1990; Swann & Taylor, 1993; Hinkle et al., 1994), lichens (Gargas et al., 1995), bryophytes (Mishler et al., 1994; Capesius, 1995; Kranz et al., 1995), gymnosperms (e.g., Chaw et al., 1993, 1995, 1997), and even among the deepest branches of life (Wolters & Erd-

[2] Department of Botany, Washington State University, Pullman, Washington 99164, U.S.A.
[3] Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901, U.S.A.
[4] Laboratory of Molecular Systematics, Smithsonian Institution, Washington, D.C. 20560, U.S.A.
[5] Department of Biological Sciences, University of Wisconsin, Milwaukee, Wisconsin 53201, U.S.A.
[6] Department of Biology, Wake Forest University, Winston-Salem, North Carolina 27109, U.S.A.
[7] Laboratory of Molecular Systematics, Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AB, United Kingdom.
[8] Department of Biology, Ithaca College, Ithaca, New York 14850, U.S.A.
[9] Institute of Botany, Academia Sinica, Nankang, Taipei, Taiwan, Republic of China.
[10] Research Division, Canadian Museum of Nature, Ottawa, Ontario K1P 64P, Canada.
[11] Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.
[12] Department of Botany, University of Wisconsin, Madison, Wisconsin 53706, U.S.A.

mann, 1986; Olsen, 1987; Woese, 1987; Embley et al., 1994; Bhattacharya & Medlin, 1995).

Despite this wide usage in other major groups of organisms, the 18S rRNA gene has received comparatively little attention in angiosperms. In large part this reflects the enormous interest in, and demonstrated utility of, *rbc*L sequences for inferring phylogeny, particularly at the family level and above (e.g., Chase et al., 1993; Morgan & Soltis, 1993; Olmstead et al., 1993; Kron & Chase, 1993; Qiu et al., 1993; Rodman et al., 1993). In addition, skepticism apparently exists among many angiosperm systematists regarding the utility of 18S rDNA sequences for inferring plant phylogeny. Early analyses of 18S rDNA or rRNA sequences in angiosperms (e.g., Nickrent & Franchina, 1990; Hamby & Zimmer, 1992; Nickrent & Starr, 1994), while in general pointing to the possibile phylogenetic utility of these data, raised concerns that 18S rDNA may be too evolutionarily conservative to address phylogenetic questions at the family level and above and that insertion and deletion events (indels) occur frequently in at least some portions of 18S rDNA, making alignment of sequences difficult. In addition, other basic background information regarding the molecular evolution of the 18S rRNA gene is not available for angiosperms. For example, given that 18S rRNA, as well as rRNAs in general, have inherent secondary structure that includes characteristic loop (non-paired) and stem (paired) stretches of RNA, should changes in the encoding stem and loop bases be considered equally informative in phylogenetic analyses? Models of rRNA evolution suggest that paired (stem) bases will undergo compensatory changes to maintain the appropriate base pairing. However, empirical studies of angiosperm rRNA structure are few (e.g., Senecoff & Meagher, 1992), and available data sets have not been used to evaluate patterns of evolution of the 18S rRNA gene in angiosperms.

The history of the use of 18S rRNA and rDNA sequences for phylogeny reconstruction in angiosperms was recently reviewed (Nickrent & Soltis, 1995). To date, the largest studies of 18S sequences are those of Hamby and Zimmer (1992) and Nickrent and Soltis (1995). Zimmer and collaborators conducted phylogenetic analyses using direct sequencing of rRNA from approximately 60 species of vascular plants, of which 29 were dicots and 17 monocots (Zimmer et al., 1989; Hamby & Zimmer, 1992). These investigators sequenced portions of both 18S and 26S rRNA, yielding a total of 1701 base positions per taxon, 1097 base positions from the 18S gene and 604 from the 26S gene. The shortest trees obtained had a number of features in accord with existing classifications, but sampling of nonmagnoliid taxa was sparse and may explain some of the unusual relationships suggested among more derived angiosperms. Furthermore, many of the nodes were poorly supported. As a result of the unusual relationships suggested for some taxa and the poor resolution obtained in this study, angiosperm systematists remained unsure of the utility of 18S and 26S rRNA (and rDNA) sequences for inferring phylogeny.

More recently, Nickrent and Soltis (1995) compared the rate of evolution and phylogenetic resolution of entire 18S rDNA sequences with those for the chloroplast gene *rbc*L using a taxonomically similar suite of 59 angiosperms. Pairwise comparisons showed that *rbc*L is generally about three times more variable than 18S rDNA. However, because of the longer length of 18S rDNA, the ratio of the number of phylogenetically informative sites per molecule is only about 1.4 times greater for *rbc*L than for 18S rDNA. Exploratory parsimony analyses of angiosperms showed that several clades were strongly supported by both *rbc*L and 18S rDNA data sets. Nickrent and Soltis (1995) concluded that complete 18S rDNA sequences are sufficiently variable to conduct phylogenetic studies at higher levels within the angiosperms.

Here we explore further the higher-level phylogenetic relationships within the angiosperms using entire nuclear 18S rDNA sequences. More specifically, we provide phylogenetic hypotheses for flowering plants based on analyses of four 18S rDNA data sets, differing in both the number of taxa and the inclusion of indels as additional characters. We also compare the phylogenetic estimates based on 18S rDNA sequences with those obtained from phylogenetic analysis of *rbc*L sequences (Chase et al., 1993). Using the phylogenetic estimates, we examine patterns of molecular evolution of 18S rDNA by assessing the frequency of insertions and deletions, the prevalence of compensatory changes, and the relative phylogenetic importance of stem versus loop changes in angiosperm 18S rDNA.

Materials and Methods

Species Sampled and Sources of Plant Material

The species included in this analysis are given in Table 1, along with family membership, general collection information, and GenBank accession numbers for the 18S sequences. In Table 1, and throughout the text, we generally follow the taxonomic circumscriptions of Cronquist (1981) for dicots and Dahlgren et al. (1985) for monocots. This

Table 1. Species analyzed for 18S rDNA sequence variation. Species are arranged alphabetically by families (dicots according to Cronquist; monocots according to Dahlgren). Within families, species are arranged alphabetically by genus. † indicates those angiosperms present in the 228-taxon data sets, but not the 199-taxon data sets.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Pachystachys lutea Nees	Acanthaceae	*Johnson 95-003*, WS		U49290	Johnson
Acer rubrum L.	Aceraceae	*Soltis & Soltis 2515*, WS		U42494	Soltis
Actinidia sp.	Actinidiaceae	*Morgan s.n.*, WS		U42495	Soltis
Tetragonia expansa Murr.	Aizoaceae	*Hershkovitz 111*, WS		U42496	Soltis
Sagittaria trifoliata L.	Alismataceae	*Chau 1371*, HAST		D29781	Chaw
† *Allium thunbergii* G. Don	Alliaceae	NA 55049, US		U42071	Hahn & Kress
† *Eucharis grandiflora* Planch & Linden	Amaryllidaceae	*Hahn 6868*, WIS		U42069	Hahn
Hippeastrum sp.	Amaryllidaceae	*Hahn 6875*, WIS		U42065	Hahn
Amborella trichopoda Baill.	Amborellaceae	*Suh 44*, US		U42497	Soltis & Soltis
† *Isolona* sp.	Annonaceae	*Chase 542*, K		L54061	Chase
Mkilua fragrans	Annonaceae	*Schatz 3364*, WIS		L54060	Hoot
Chlorophytum nepalense Baker	Antheriaceae	*Kress 92-3434*, US		U42066	Hahn & Kress
Lomatium triternatum (Pursh) Coult. & Rose	Apiaceae	*Soltis 2266*, WS		U42498	Soltis & Soltis
Tabernaemontana divaricata (L.) R. Br.	Apocynaceae	*Nickrent 2978*, SIU		U42499	Soltis & Soltis
† *Acorus calamus* L.	Araceae	*Nickrent 2941*, SIU	Nickrent & Soltis, 1995	L24078	Nickrent
Calla palustris L.	Araceae	*Hahn 6959*, WIS		U42073	Hahn
Veitchia sessilifolia Burret	Arecaceae	*Hahn*, US		U42070	Hahn
Hedera helix L.	Araliaceae	*Plunkett 1368*, WS		U42500	Soltis & Soltis
Aristolochia tomentosa Sims.	Aristolochiaceae	*Nickrent 2922*, SIU	Nickrent & Soltis, 1995	L24083	Nickrent
Asarum canadense L.	Aristolochiaceae	*Nickrent 2888*, SIU	Nickrent & Starr, 1994	L24043	Nickrent
† *Saruma henryi* Oliver	Aristolochiaceae	*Qiu 91018*, NEU	Nickrent & Soltis, 1995	L24417	Nickrent
Tagetes sp.	Asteraceae	*Nickrent 3061*, SIU		U42501	Soltis & Soltis
Tragopogon dubius Scop.	Asteraceae	*Soltis 2472*, WS		U42502	Soltis & Soltis
Austrobaileya scandens C. T. White	Austrobaileyaceae	*Nickrent 2953*, SIU		U42503	Nickrent
Impatiens wallerana Hook.	Balsaminaceae	*Johnson 95-071*, WS		U49285	Johnson
Batis maritima L.	Bataceae	*Ilis 30500*, WIS		U42504	Soltis & Soltis

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Bauera rubioides Andrews	Baueraceae	*Kew 1977-6377*, K		U42505	Soltis
Begonia metallica × *sanguinea*	Begoniaceae	*Chase 225*, NCU		U42506	Soltis
Symbegonia sp.	Begoniaceae	*Kew U012*, K		U43613	Swensen
Caulophyllum thalictroides (L.) Michx.	Berberidaceae	*Hoot 925*, UWM		L54064	Hoot
† *Podophyllum peltatum* L.	Berberidaceae	*Nickrent 2891*, SIU		L24413	Nickrent
Alnus glutinosa L. Gaertn.	Betulaceae	unknown	Savard & Lalonde, 1991	X59984	
Parmentiera cerifera Seem.	Bignoniaceae	*Johnson 95-005*, WS		L49291	Johnson
Bombax ceiba Burm.	Bombacaceae	*Alverson s.n.*, WIS		U42507	Kuzoff
Bourreria succulenta Jacq.	Boraginaceae	*J. Miller 6421*, MO		U38319	Nickrent
Arabidopsis thaliana (L.) Heyn.	Brassicaceae	unknown	Unfried et al., 1989	X16077	
Brassica hirta Moench	Brassicaceae	unknown	Rathgeber & Capesius, 1990	X17062	
Glomeropitcairnia penduliflora (Grisebach) Mez	Bromeliaceae	*Kress 92-3466*, US		U42075	Hahn & Kress
Berzelia lanuginosa (L.) Brongn.	Bruniaceae	*Price s.n.*, IND		U42508	Soltis
Buddleja davidii Franch.	Buddlejaceae	*Johnson 95-031*, WS		L49275	Johnson
Buxus sempervirens L.	Buxaceae	*Hoot 921*, UWM		L54065	Hoot
Byblis gigantea	Byblidaceae	Palmengarten B. G.		U42509	Soltis & Soltis
Calycanthus floridus L.	Calycanthaceae	*Nickrent 2893*, SIU		U38318	Nickrent
Campanula ramulosa Wall.	Campanulaceae	*Jansen 984*, MICH		U42510	Soltis & Soltis
Lobelia erins L.	Campanulaceae	*Jansen 989*, MICH		U42785	Soltis & Soltis
Canna coccinea Mill.	Cannaceae	*Chaw 1371*, HAST		D29784	Chaw
Cleome hasleriana Chodat	Capparaceae	*Al-Shehbaz, s.n.*, MO		U42511	Soltis & Soltis
Koeberlinia spinosa Zucc.	Capparaceae	*Al-Shehbaz, s.n.*, MO		U42512	Soltis & Soltis
† *Lonicera maackii* (Rupr.) Maxim.	Caprifoliaceae	*Nickrent 3060*, SIU		U66701	Soltis & Soltis
Symphoricarpos albus (L.) Blake	Caprifoliaceae	*Olmstead s.n.*, COLO		U42513	Soltis & Soltis
Carica papaya L.	Caricaceae	Missouri B. G., MO		U42514	Soltis & Soltis
Casuarina equisetifolia L.	Casuarinaceae	*Nickrent 2977*, SIU		U42515	Soltis
Euonymus alatus (Thunb.) Sieb old	Celastraceae	*Nickrent 2894*, SIU	Nickrent & Franchina, 1990	X16600	Nickrent
Cephalotus folicularis Labill.	Cephalotaceae	*Chase 147*, NCU		U42516	Soltis
Ceratophyllum demersum L.	Ceratophyllaceae	*Qiu 91027*, NCU		U42517	Soltis

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Cercidiphyllum japonicum Siebold & Zucc.	Cercidiphyllaceae	*Soltis 2540*, WS		U42518	Soltis
Spinacia oleracea L.	Chenopodiaceae	*Nickrent 2896*, SIU	Nickrent & Soltis, 1995	L24420	Nickrent
Hedyosmum arborescens Sw.	Chloranthaceae	*Nickrent 3022*, SIU		U38536	Nickrent
Chrysobalanus icaco L.	Chrysobalanaceae	Fairchild Trop. G 76-311		U42519	Soltis
Licania tomentosa Fritsch	Chrysobalanaceae	Fairchild Trop. B. G. 64-734		U42520	Soltis
Clethra alnifolia L.	Clethraceae	*Kron 1884s*, NCU		U42521	Soltis
Colchicum autumnale L.	Colchicaceae	*Hahn 6864*, WIS		U42072	Hahn
Elasis sp.	Commelinaceae	*Evans s.n.*, WIS		U42076	Hahn
Ipomoea hederacea Jacq.	Convolvulaceae	*Colwell s.n.*, MO		U38310	Nickrent
Aucuba japonica Thunb.	Cornaceae	U.S. Natl. Arb.		U42522	Soltis
Corokia cotoneaster Raoul	Cornaceae	Strybing Arb. 74211		U42523	Soltis & Soltis
Helwingia japonica (Thunb.) F. Dietr.	Cornaceae	Arnold Arb. 912		U42524	Soltis & Soltis
Costus barbatus Suess.	Costaceae	*Kress 94-3710*, US,		U42080	Hahn & Kress
Crassula marnierana Huber & Jacobsen	Crassulaceae	*Morgan 2152*, WS		U42525	Soltis
Dudleya viscida (S. Watson) Moran	Crassulaceae	Huntington B. G. 62801		U42526	Soltis
Kalanchöe diagremontana Hamet & Perrier	Crassulaceae	*Morgan 2151*, WS		U42527	Soltis
Sedum rubrotintum Clausen	Crassulaceae	*Morgan 2153*, WS		U42528	Soltis
Crossosoma californicum Nutt.	Crossosomataceae	Rancho Santa Ana B. G.		U42529	Soltis
Abobra tenuiflora Naudin.	Cucurbitaceae	*Chase 915*, K		U41501	Swensen
Ceratopetalum gummiferum Small	Cunoniaceae	*Keller 2135*, CAS		U42530	Soltis
Cuscuta gronovi Willd.	Cuscutaceae	*Nickrent 3015*, SIU	Nickrent & Soltis, 1995	L24747	Nickrent
Cyperus albostriatus Schrader	Cyperaceae	*Kress 92-3463*, US		U42077	Hahn & Kress
† *Cyrilla racemifolia* L.	Cyrillaceae	*Kron s.n.*, NCU	Kron, 1996	U43294	Kron
Daphniphyllum sp.	Daphniphyllaceae	*Qiu 91026*, NCU		U42531	Soltis
Datisca glomerata (Presl) Baill.	Datiscaceae	Rancho Santa Ana B. G.		U42426	Swensen

Table 1. Continued.

	Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
	Tetrameles nudiflora R. Br.	Datiscaceae	Central B. G., Sara Bori, Thailand; *Philbrick & Wongprasert 2272*		U41502	Swensen
	Diapensia lapponica L.	Diapensiaceae	*Hills 89018*, NCU		L49278	Johnson
	Galax urceolata L.	Diapensiaceae	*Kron 163*, NCU		L49281	Johnson
†	*Dillenia alata* (DC) Mart.	Dilleniaceae	*Nickrent 2956*, SIU		U38314	Nickrent
	Dipsacus sp.	Dipsacaceae	*Jansen 931*, MICH		U43150	Soltis & Soltis
	Drosera capensis	**Droseraceae**	**Palmengarten B. G.**		**U42532**	Soltis
†	*Diospyros virginiana* L.	Ebenaceae	*Kron 3004*, NCU		U43295	Kron
	Elaeagnus umbellata Thunb.	Elaeagnaceae	*Nickrent 2898*, SIU		L24090	Nickrent
	Sloanea cf. *latifolia* K. Sch.	Elaeocarpaceae	*Alverson s.n.*, WIS		U42826	Kuzoff
	Ephedra aurea Stapf	Ephedraceae	TI-9297, TI		D38242	Chaw
	Ephedra torreyana S. Wats.	Ephedraceae	*Gillespie 4236*, US		U42414	Sweere
	Arctostaphylos uva-ursi (L.) Spreng.	Ericaceae	*Johnson 94-085*, WS		L49272	Johnson
	Vaccinium macrocarpon Ait.	Ericaceae	*Kron 2937*, NCU		L49297	Johnson
†	*Eucommia ulmoides* Oliv.	Eucommiaceae	*Qiu 91024*, NCU		L54066	Hoot
	Eucryphia lucida Druce	Eucryphiaceae	Strybing Arb. 86-0250		U42533	Soltis
	Drypetes roxburghii (Wall.) Hurus.	Euphorbiaceae	FTG-83463A, K		U42534	Soltis
	Euphorbia pulcherima	Euphorbiaceae	*Soltis & Soltis 2541*, WS		U42535	Soltis
	Euptelea polyandra Siebold & Zucc.	Eupteleaceae	*Qiu 9001*, NCU		L75831	Hoot
	Albizia julibrissin Durazz.	Fabaceae	*Doyle 1526*, BH		U42536	Soltis
	***Bauhinia* sp.**	**Fabaceae**	***Doyle s.n.*, MSU**		**U42537**	Soltis
†	*Glycine max.* (L.) Merrill	Fabaceae	unknown	Eckenrode et al., 1985	X02623	
	Pisum sativum L.	Fabaceae	Carolina Biological Laboratory, Burlington N.C.		U43011	Sweere
*	*Muntingia calabura* Griseb.	Flacourtiaceae	*Alverson 2172*, WIS		U42539	Kuzoff
	Dicentra exima Torrey	Fumariaceae	*Reznicek 9756*, MICH		L37908	Hoot
	Fouquieria splendens Engelm.	Fouquieriaceae	Missouri B. G. 860162, MO		L49280	Johnson
	Garrya elliptica Douglas ex Lind.	Garryaceae	Rancho Santa Ana B. G. 13280		U42540	Soltis
	Geranium cinereum Cav.	Geraniaceae	*Price s.n.*, IND		U42541	Soltis

*A recent detailed phylogenetic analysis of Flacourtiaceae using *rbc*L sequences indicates that *Muntingia* is only distantly related to the "true" flacourts (Chase, unpublished).

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Aeschynanthus radicans Jack.	Gesneriaceae	*Nickrent 2979*, SIU		U42542	Soltis & Soltis
Gnetum gnemon L.	Gnetaceae	*Gillespie 4212*, US		U42416	Sweere
Gnetum nodiflorum Brongn.	Gnetaceae	*Gillespie 4246*, US		U42415	Sweere
Gnetum urens (Aubl.) Blume	Gnetaceae	*Kress et al. 91-3271*, US		U42417	Sweere
Greyia radlkoferi Szyszyl.	Greyiaceae	Strybing Arb. 640406		U43151	Soltis
Brexia madagascarensis Thouars ex Ger Gawl.	Grossulariaceae	Kew 1977-14901, K		U42543	Soltis
Escallonia coquimbensis Reamy	Grossulariaceae	U. Calif. B. G. 52-1333		U42544	Soltis & Soltis
Itea virginica L.	Grossulariaceae	*Ware 9401*, WS		U42545	Soltis
Phyllonoma laticuspus (Turcz.) Engl.	Grossulariaceae	*Morgan 2124*, WS		U42546	Soltis
Pterostemon rotundifolius Ramirez	Grossulariaceae	*Sanchez 259*, TEX		U42547	Soltis
Ribes aureum Pursh	Grossulariaceae	*Soltis & Soltis 2220*, WS		L28143	Soltis
Roussea simplex J. E. Smith	Grossulariaceae	Herbarium, Mauritius Sugar Ind. Res. Inst.		U42548	Soltis
Tetracarpaea tasmanica Hook f.	Grossulariaceae	*Jordan s.n.*, HO		U42549	Soltis
Gunnera manicata Linden	Gunneraceae	*Kruckeberg s.n.*, WTU		U43787	Soltis
Haloragis erecta (Banks ex Murr.) Eichler	Haloragaceae	*Chase 453*, K		U42550	Soltis
Altingia sp.	Hamamelidaceae	RBG, Edinburgh, Qiu 93006		U42552	Soltis
Liquidambar styraciflua L.	Hamamelidaceae	*Soltis & Soltis 2516*, WS		U42553	Soltis
Heliconia indica Lamark	Heliconiaceae	*Kress 80-1118*, US		U42082	Hahn & Kress
Bowiea volubilis Harvey ex. Hook f.	Hyacinthaceae	*Hahn 6882*, WIS		U42067	Hahn
Hydrangea macrophylla Torr.	Hydrangeaceae	*Morgan 2150*, WS		U42781	Soltis
Philadelphus lewisii Pursh.	Hydrangeaceae	*Soltis & Soltis 2411*, WS		U42782	Soltis
Phacelia bicolor Torr. ex Wats.	Hydrophyllaceae	*Johnson 92-005*, WS		L49292	Johnson
Illicium parviflorum Michx. ex Vent.	Illiciaceae	*Naczi 2784*, MICH		L75832	Hoot
Gladiolus buckevildii (L. Bol.) Goldblatt	Iridaceae	*Goldblatt & Manning 9504*, MO		L54062	Hoot
† *Isophysis tasmanica* (Hook.) T. Moore	Iridaceae	*J. Bruhl s.n.*, TAS		L64063	Hoot
Lactoris fernandeziana Phil.	Lactoridaceae	*Steussy et al. 11.784*, OSU		U42783	Soltis

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Lamium amplexicaule L.	Lamiaceae	*Johnson 95-001*, WS		L49287	Johnson
Akebia quinata (Houtt.) Decne.	Lardizabalaceae	*Nickrent 2945*, SIU		L31795	Nickrent
Sassafras albidum (Nutt.) Nees	Lauraceae	*Soltis & Soltis 2518*, WS			
† *Lilium formosanum* Wallace	Liliaceae	H0962, HAST		D29775	Chaw
Floerkea proserpinicoides Willd.	Limnanthaceae	*Reznicek 8609*, MICH		U42784	Soltis & Soltis
Linum perenne L.	Linaceae	*Nickrent 2900*, SIU		L24401	Nickrent
Malpighia coccigera L.	Malpighiaceae	*Nickrent 2905*, SIU		L24046	Nickrent
Gossypium hirsutum L.	Malvaceae	*Alverson s.n.*, WIS		U42827	Kuzoff
Maranta bicolor Vell.	Marantaceae	*Kress 94-3724*, US		U42079	Hahn & Kress
Menispermum canadensis L.	Menispermaceae	*Naczi 2837*, MICH		L75834	Hoot
† *Tinospora caffra* Miers	Menispermaceae	*Jaarsveld 2131*, NBG		L37914	Hoot
Mollugo verticillata L.	Molluginaceae	*Hershkovitz 37*, WS		U42828	Kuzoff
† *Monotropa uniflora* L.	Monotropaceae	*Nickrent 3018*, SIU	Nickrent & Soltis, 1995	L25680	Nickrent
Morus alba L.	Moraceae	*Nickrent 2924*, SIU		L24398	Nickrent
Moringa oleifera Lam.	Moringaceae	*Iltis 30501*, WIS		U42786	Soltis & Soltis
Musa acuminata Colla	Musaceae	U.S. Bot. Gard. *s.n.*, US		U42083	Hahn & Kress
Nelumbo lutea (Willd.) Pers.	Nelumbonaceae	*Hoot 9212*, 1713		L75835	Hoot
Nepenthes sp.	Nepenthaceae	*Nickrent 3056*, SIU		U42787	Soltis
Nymphaea tuberosa Paine	Nymphaeaceae	*Nickrent 2906*, SIU	Nickrent & Soltis, 1995	L24404	Nickrent
Mirabilis jalapa L.	Nyctaginaceae	*Hershkovitz 60*, WS		U42788	Soltis
Camptotheca acuminata Decne.	Nyssaceae	*Strybing Arb.* 74-180		U42789	Soltis & Soltis
Olea europaea L.	Oleaceae	*Johnson 95-004*, WS		L49289	Johnson
† *Clarkia xantiana* A. Gray	Onagraceae	*Gottlieb 7436*, DAV		U67930	Sytsma
Opilia amentacea Roxb.	Opiliaceae	*Nickrent 2816*, SIU		U42790	Soltis
Oncidium excavatum Lindl.	Orchidaceae	*Chase 83427*, K		U42791	Soltis
Paeonia suffructicosa	Paeoniaceae	*Chase 486*, K		U42792	Soltis
Hypecoum imberba Sm.	Papaveraceae	*Chase 528*, K		L75836	Hoot
Helmholtzia sp.	Philydraceae	*Kress 92-3505*, US		U42074	Hahn & Kress
Phytolacca americana L.	Phytolaccaceae	*Hershkovitz 38*, WS		U42793	Soltis
Peperomea serpens (Swartz) Loud.	Piperaceae	*Nickrent 2907*, SIU	Nickrent & Soltis, 1995	L24411	Nickrent

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Pittosporum japonicum Hort. ex C. Presl.	Pittosporaceae	*Rieseberg s.n.*, RSA	Nickrent & Soltis, 1995	L28142	Soltis & Kuzoff
Platanus occidentalis L.	Platanaceae	*Soltis & Soltis 2514*, WS		U42794	Sweere, Zimmer, & Soltis
Plumbago auriculata Lam.	Plumbaginaceae	*Nickrent s.n.*, SIU		U42795	Kuzoff
Oryza sativa L.	Poaceae	unknown	Takaiwa et al., 1984	X00755	Takaiwa et al., 1984
Zea mays L.	Poaceae	(Genomic DNA) Clontech Laboratories, Inc., Palo Alto, CA		U42796	Sweere, Zimmer, & Soltis
Acanthogilia gloriosa (Brandegee) A. G. Day & Moran	Polemoniaceae	*Johnson & Mort, 95-070*, WS		L49271	Johnson
Cobaea scandens Cav.	Polemoniaceae	*Patterson s.n.*, WS		L49277	Johnson
Gilia capitata Sims.	Polemoniaceae	*Johnson 92-15*, WS	Nickrent & Soltis, 1995	L24143	Soltis & Kuzoff
Polygala pauciflora Willd.	Polygalaceae	*Doyle 1567*, BH		U42797	Soltis
Cocoloba uvifera L.	Polygonaceae	*Nickrent 2927*, SIU		U42798	Sweere, Zimmer, & Soltis
Primula sp.	Primulaceae	*Johnson 95-006*, WS		L49295	Johnson
Knightia excelsa R. Br.	Proteaceae	Univ. of California, Santa Clara, B. G.	Nickrent & Soltis, 1995	L24155	Nickrent
† *Placospermum coriaceum* C. T. White & W. D. Francis	Proteaceae	*Douglas 110*, MEL		L75837	Hoot
† *Punica granatum* L.	Punicaceae	*Nickrent 2931*, SIU		U38311	Nickrent
† *Pyrola picta* Sm.	Pyrolaceae	*Colwell, s.n.*, MO			Colwell & Nickrent
† *Coptis trifolia* (L.) Salisb.	Ranunculaceae	*Voss & Howard*, MICH		L75838	Hoot
Ranunculus sardous Crantz	Ranunculaceae	*Nickrent 2932*, SIU	Nickrent & Soltis, 1995	L24092	Nickrent
Xanthorhiza simplicissima Marshall	Ranunculaceae	*Qiu 91030*, NCU		L75839	Hoot
Ceanothus sanguineus Pursh	Rhamnaceae	*Morgan 2155*, WS		U42799	Soltis

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
Photinia fraseri Dress	Rosaceae	*Morgan 2131*, WS		U42800	Soltis
Prunus persica (L.) Batsch	Rosaceae	*E. E. Dickson s.n.*, BH		L28749	Soltis
Spiraea vanhoutei (Briot) Zubel	Rosaceae	*Morgan 2130*, WS		U42801	Soltis
Mitchella repens L.	Rubiaceae	*Xiang s.n.*, OSU		U42802	Soltis & Soltis
† *Citrus aurantium* L.	Rutaceae	*Nickrent 2977*, SIU		U38312	Nickrent
Sabia swinhoei	Sabiaceae	*Wagner 6518*, HAST		L75840	Hoot
Osyris lanceolata Hochst. & Steud.	Santalaceae	*Nickrent 2731*, SIU		U42803	Soltis
† *Koelreuteria paniculata* Laxm.	Sapindaceae	*Nickrent 2915*, SIU		U38313	Nickrent
Manilkara zapota (L.) Royen	Sapotaceae	*Chase 129*, NCU	Kron, 1996	U43080	Kron
† *Sargentodoxa cuneata* (Oliv.) Rehdes & Wil.	Sargentodoxaceae	*Qiu s.n.*, PE		L75841	Hoot
Sarracenia purpurea L.	Sarraceniaceae	*Morgan s.n.*, WS		U42804	Soltis
Houttuynia cordata Thunb.	Saururaceae	*Nickrent 2940*, SIU	Nickrent & Soltis, 1995	L24147	Nickrent
Saururus cernuus L.	Saururaceae	*Suh 128*, US		U42805	Sweere, Zimmer & Soltis
Boykinia intermedia (Piper) Jones	Saxifragaceae	*Grable 11638*, WS		U42806	Soltis
Eremosyne pectinata Endl.	Saxifragaceae	*Annels & Hearn 4795*, PERTH		U42807	Soltis
Francoa sonchifolia Cav.	Saxifragaceae	*Soltis & Soltis 2479*, WS	Nickrent & Soltis, 1995	L28137	Soltis
Heuchera micrantha Douglas	Saxifragaceae	*Soltis & Soltis 1949*, WS		X28139	Soltis
Lepuropetalon spathulatum (Muhl.) Elliott	Saxifragaceae	*Thomas s.n.*, NLU		L28141	Soltis
Montinia caryophyllacea Thunb.	Saxifragaceae	*Williams 2833*, MO		U42808	Soltis & Soltis
Parnassia fimbriata Banks	Saxifragaceae	*Soltis & Soltis s.n.*, WS		U42809	Soltis
Penthorum sedoides L.	Saxifragaceae	*Hayden 2232*, WS		U25660	Soltis
Saxifraga integrifolia Hook.	Saxifragaceae	*Soltis & Soltis 2253*, WS		U42810	Soltis
Vahlia capensis Thunb.	Saxifragaceae	*Van Wyk 10-579*, PRU		U42813	Soltis & Soltis
Schisandra chinesis (Turcz.) Baill.	Schisandraceae	*Reznicek s.n.*, MICH		L75842	Hoot
† *Linaria vulgaris* P. Mill	Scrophulariaceae	*Colwell* MO CA1, SIU		U38315	Colwell & Nickrent

Table 1. Continued.

Species	Family	Voucher/source	Literature citation	Genbank	Sequence by
† *Orthocarpus erianthus* Benth.	Scrophulariaceae	*Colwell* CA SVD10, SIU		U38316	Colwell & Nickrent
† *Pedicularis lanceolata* Michx.	Scrophulariaceae	*Colwell* MO SFP1, SIU		U38317	Colwell & Nickrent
Brunfelsia pauciflora (Cham. & Schlechtend.) Benth.	Solanaceae	*Johnson 95-002*, WS		L49274	Johnson
† *Sparganium eurycarpum* Engl.	Sparganiaceae	*Nickrent 2943*, SIU	Nickrent & Soltis, 1995	L24419	Nickrent
† *Styrax americana* Lam.	Styracaceae	*Kron 3002*, NCU	Kron, 1996	U43296	Kron
Symplocos paniculata Miq.	Symplocaceae	*Kron 3005*, NCU	Kron, 1996	U43297	Kron
Tacca sp.	Taccaceae	Missouri Bot. Garden 894904, US		U42063	Hahn
Cyanella capensis L.	Tecophilaeaceae	*Hahn 6966*, WIS		U42078	Hahn
Tetracentron sinensis Oliv.	Tetracentraceae	*Qiu 90009*, NCU		U42814	Soltis
Camelia japonica L.	Theaceae	*Nickrent 2929*, SIU		U42815	Soltis
Luehea seemannii Cuatr.	Tiliaceae	*Alverson 2184*, WIS		U42829	Kuzoff
Trochodendron aralioides Siebold & Zucc.	Trochodendraceae	*Qiu 90026*, NCU		U42816	Soltis
Tropaeolum majus L.	Tropaeolaceae	*Chase 113*, NCU	Nickrent & Soltis, 1995	L31796	Soltis
Turnera ulmifolia	Turneraceae	*Chase 220*, NCU		U42817	Soltis
Celtis yunnanensis C. K. Schneid.	Ulmaceae	*Qiu P90002*, NCU		U42818	Soltis
Zelkova serrata	Ulmaceae	*Soltis & Soltis 2517*, WS		U42819	Soltis
Pilea cadierei Gagnep. & Guillam.	Urticaceae	*Nickrent 2972*, SIU		U42820	Soltis
Viscum album L.	Viscaceae	*Nickrent 2253*, SIU		U42821	Soltis
Drimys aromatica	Winteraceae	*Suh 9*, US		U42822	Soltis & Soltis
Drimys winteri J. R. & G. Forster	Winteraceae	*Suh 47*, US		U42823	Sweere, Zimmer, & Soltis
Xanthorrhoea sp.	Xanthorrhoeaceae	*Kress 92-3422*, US		U42064	Hahn & Kress
Zamia pumila L.	Zamiaceae	unknown	Nairn & Ferl, 1988	M20017	Nairn & Ferl
Zingiber gramineum Noronha	Zingiberaceae	*Kress 91-3266*, US		U42081	Hahn & Kress
Guaiacum sanctum L.	Zygophyllaceae	*Anderson s.n.*, MICH		U42824	Soltis

approach parallels that in Chase et al. (1993) and should facilitate comparison.

As with the broad analyses of *rbc*L sequences, close examination of the genera included in this study will reveal an uneven taxonomic distribution. Some groups are relatively well represented (e.g., Saxifragaceae sensu stricto [Saxifragaceae s. str.] and allies, ranunculids, Asteridae sensu lato [Asteridae s.l.]), whereas others are not as thoroughly sampled (e.g., portions of Dilleniidae and Magnoliidae). However, our selection of taxa was not random. We attempted to include samples from all major angiosperm orders and subclasses sensu Cronquist (1981). Furthermore, in selecting genera for sequencing, we tried to sample representatives from each of the major clades recovered in the analyses of Chase et al. (1993) (e.g., rosid I, asterid I, asterid III, etc.), as well as from the various subclades present within those major clades. We also used, when available, the same DNAs used previously for the sequencing of *rbc*L (Chase et al., 1993). If a given DNA was no longer available, we attempted to obtain leaf material of the same species, and if that failed, from a congeneric species.

Another factor that influenced our choice of taxa was sequence quality. As discussed in detail below, one outcome of this study was the discovery that many available sequences are erroneous, some highly so. We therefore attempted to eliminate any dubious sequences from our data sets. In addition, some available sequences were not included because they were incomplete or contained numerous ambiguities or extensive gaps.

Several laboratories were involved in this project; hence, several different protocols were used to generate the sequences analyzed. Although both automated and manual sequencing strategies were employed, 70% of the sequences analyzed were generated via automated sequencing. The general methods used for PCR amplification and subsequent manual sequencing of 18S rDNA are provided in Nickrent (1994), Nickrent and Starr (1994), and Bult et al. (1992). General methods for the automated sequencing approach for 18S rDNA are given in D. Soltis and Soltis (1997). The base composition of the oligonucleotide primers used for PCR and sequencing are provided in Nickrent and Starr (1994) and Bult et al. (1992).

ALIGNMENT OF THE 18S rDNA SEQUENCES

With the exception of a few, small, well-defined regions, alignment of 18S rDNA sequences was easily accomplished by eye across all taxa. This general ease of alignment is due not only to the highly conserved nature of the 18S rRNA gene, but also to the fact that most length mutations involve insertions or deletions of a single base pair. Straightforward alignment of sequences was further facilitated by the fact that most indels in 18S rDNA are confined to a few specific regions that are particularly prone to variation in primary sequence and length, such as the termini of helices E10-1, 17, E23-1, and 43 (see also Nickrent & Soltis, 1995). Because they were difficult to align over a broad taxonomic scale, no attempt was made to align four small regions of 18S rDNA over all of the taxa analyzed: positions 230-237; 496-501; 666-672; 1363-1369 (see Appendix). These base positions correspond to the sequence of *Glycine max* (Eckenrode et al., 1985), which provides a convenient reference sequence because of the availability of a proposed ribosomal RNA secondary structure model (Nickrent & Soltis, 1995). These four regions of ambiguous alignment were subsequently eliminated from the phylogenetic analyses, following Swofford and Olsen (1990). In addition, the extreme 5′ and 3′ ends of the sequences were not included in the analyses. Positions 1–20 were excluded because they correspond to the forward PCR primer. Because most of the sequences were clearly readable at, or just before, base position 41, we began analysis of our data set at position 42. At the 3′ end of the 18S sequences, base positions 1751–1808 (on *Glycine*) were often difficult to read and also were eliminated from the analysis. Some sequences are incomplete at the 3′ end and are approximately 1700 base pairs in length. The total length of the aligned 18S rDNA sequences was 1850 base pairs.

Two indels, each of a single base pair, were detected in highly conserved regions of the 18S rRNA gene not prone to insertion-deletion (Table 2). One indel (A), an apparent deletion based on outgroup comparison, is present in all higher dicots (i.e., the large clade consisting of Rosidae and Asteridae s.l.). A second indel (B), an apparent insertion, occurs in all members of the saxifragoid clade (also referred to as Saxifragales; D. Soltis & Soltis, 1997). These two indels were included as characters in two of the phylogenetic analyses, as described below.

PHYLOGENETIC ANALYSIS

We constructed four data sets for phylogenetic analysis: (1) a data set of 223 angiosperms plus five members of Gnetales as outgroups, without the two indels noted above; (2) taxon sampling as in (1), but with indels A and B (see also Table 2) included;

Table 2. Potentially phylogenetically informative indels located in conserved regions of 18S rNDA. Indel A is one-bp deletion that characterizes all higher eudicots (i.e., the Rosidae and Asteridae s.l. clades). Indel B is a one-bp insertion that unites all members of the saxifragoid clade. Base positions correspond to the last position given in the sequence of *Glycine max*.

Indel A	
	1529
Glycine	CCGGGTAATCTTTG -
Trochodendron	CCGGGTAATCTTTGA
Indel B	
	1406
Glycine	TATGGCCGCTTA -GGC
Heuchera	TATGGCGATTTAAGGC

(3) a data set of 194 angiosperms, plus five Gnetales as outgroups, without the two indels; (4) taxon sampling as in (3) above, with indels A and B included. For data sets 2 and 4, the indels A and B were added to the data matrix, and the position scored as either present (1) or absent (0).

Four data sets were used for several reasons. First, the approach used permitted an assessment of the phylogenetic informativeness of the two indels. Second, our goal in constructing the two smaller data sets was to improve the phylogenetic analysis by removing incomplete and/or possibly erroneous sequences and by reducing the size of the matrix to make the problem more tractable. The two smaller data sets (3 and 4) differ from the larger data sets (1 and 2) in the removal of several taxa having long branch lengths (e.g., *Dillenia, Acorus*) and several taxa for which the sequences were incomplete (e.g., several of the ranunculids). In addition, representatives from some of the larger clades (e.g., monocots, Asteridae s.l.) and from some families for which multiple sequences were available (e.g., Annonaceae, Aristolochiaceae, Proteaceae) were removed to construct data sets 3 and 4.

The outgroups were five members of Gnetales: *Ephedra sinica, E. torreyana, Gnetum nodiflorum, G. gnemon,* and *G. urens*. Gnetales were the logical choice of outgroup because they appear as the extant sister to the angiosperms in most recent phylogenetic analyses (e.g., Crane, 1985, 1988; Doyle & Donoghue, 1986, 1992; Donoghue & Doyle, 1989a, b; Loconte & Stevenson, 1991; Chase et al., 1993; Doyle et al., 1994; Nixon et al., 1994). In addition, to ascertain the topological impact of other outgroups, particularly with regard to the first-branching angiosperms, we conducted several other searches. Using the smaller 18S data sets (194 angiosperms), both with and without indels, we used as outgroups: (1) the five Gnetales and *Zamia pumila*; (2) the five Gnetales, *Zamia pumila* and *Cycas revoluta*. Similarly, for the large data sets (223 angiosperms) we used as outgroups: (1) the five Gnetales and *Zamia pumila*; (2) the five Gnetales and a recently acquired sequence of *Welwitschia mirabilis*.

Because of the large number of taxa involved, we used two basic search strategies. The first method was a heuristic search performed using PAUP* 4.0 (Swofford, pers. comm.) and to a lesser extent PAUP 3.1.1 (Swofford, 1993) with MULPARS, RANDOM taxon addition, and TBR branch-swapping. These searches were permitted to run for a week or more using either a Macintosh Quadra 650 or Sun Sparc Server 600P. These searches did not produce trees as short as those produced by the method below and will not be discussed further.

The primary search strategy was inspired by Maddison et al. (1992) and suggested by D. Swofford (pers. comm.). For each of the four data sets, we used 50–100 consecutive searches without MULPARS using RANDOM taxon addition and NNI branch-swapping. We then performed multiple searches (300–500 replicates; a Sun Sparc Server 600P typically required 19–25 hours to complete five replicates) using RANDOM addition, MULPARS, and TBR branch swapping, where only two trees (NCHUCK = 2) of a specified length (CHUCKLEN) or longer were saved per replicate. The length of the shortest trees obtained in the NNI searches was used as the initial CHUCKLEN value. As shorter trees were found, additional searches were conducted with lower CHUCKLEN values. This approach prevented the searches from being overwhelmed with trees.

The final portion of this search strategy involved use of the shortest trees obtained above as starting points for subsequent searches, again with MULPARS and TBR branch swapping. These searches were permitted to run for weeks or months using Macintosh Quadra/Centris 650 or PowerMac 6100 or 7100 computers. Typically no more than 2000–5000 trees were saved in any of these searches. We used starting trees of several different lengths when implementing this final portion of the search strategy to explore tree space from multiple perspectives and to prevent the analysis from stalling while swapping on suboptimal trees (P. Soltis & Soltis, 1997). For data set 1, 94 starting trees of lengths 3929, 3930, 3934, 3936, 3937, 3938, 3939, 3940, and 3941 were used (shortest tree ultimately obtained had a length of 3923 steps). For data set 2, 78 starting trees of lengths 3938, 3939, 3940,

3941, 3942, 3944, 3946, and 3947 were used (shortest tree ultimately obtained had a length of 3930 steps). For data set 3, 192 starting trees of lengths 3506, 3508, 3509, 3512, 3514, 3515, and 3517 were used (shortest tree ultimately obtained had a length of 3501 steps). For data set 4, 96 starting trees of lengths 3513, 3514, 3515, 3516, 3517, 3520, and 3521 (shortest tree ultimately obtained had a length of 3507 steps). Many of these searches resulted in trees one to several steps longer than the shortest trees ultimately obtained; these longer trees were also examined to help ascertain the general support for some branches. Implementing the above search strategy for the data sets described ultimately entailed well over two years of computer time.

Implementing decay analyses (Bremer, 1988; Donoghue et al., 1992) is impractical with data sets of this size. To obtain an estimate of support for the 18S rDNA topologies, we applied the parsimony jackknife approach (Farris et al., 1997) to data set 1 (this analysis was kindly conducted by S. Farris). The jackknife is a resampling approach, similar to the bootstrap, in which the characters of a data set are resampled to generate replicate data sets. Each replicate is analyzed, and the proportion of replicates supporting a given conclusion (in this case a clade) is considered a measure of support. Jackknife percentages can therefore be interpreted similarly to bootstrap percentages. In this analysis, 1000 replicates were conducted, and a minimum jackknife value of 50 (CUT = 50) was used (i.e., only clades supported by jackknife values of 50% or greater were retained). If a node is supported by one uncontradicted character, the jackknife value is 63% (Farris et al., 1997). Thus, clades with values of 63% or more are strongly supported; nodes with values of 51–62% are less well supported, and those with values of 50% or less receive no support.

Results and Discussion

I. The Evolution of the 18S rRNA Gene

The accumulation of a large data set of entire 18S rDNA sequences has permitted a more thorough assessment of the general evolution of the 18S rRNA gene. Unlike protein-coding genes, such as the widely sequenced *rbc*L, *mat*K, and *ndh*F, there is no clear frame of reference for aligning sequences or revealing errors. For example, with protein-coding genes, translation of a sequence to amino acids will potentially reveal some errors such as frameshifts and internal stop codons. No such internal check is available, however, for rDNA. As a result, general features concerning the evolution of 18S rDNA have, in large part, been greatly misunderstood. In particular, insertion and deletion events have long been considered common in 18S rDNA; concomitantly, alignment was considered highly problematic. Until now, the existing database of angiosperm 18S rDNA sequences was insufficient to assess these views.

Insertion-Deletion and Alignment

This study reveals that indels are not widespread in the 18S rDNA sequences of angiosperms, but instead are confined to a few, small regions of the gene. Furthermore, with the exception of these same small regions, alignment of 18S rDNA sequences is straightforward. Several possibilities may explain the misconception that the 18S rRNA gene is highly prone to insertion and deletion. First, the literature contains a number of erroneous 18S rDNA sequences. We have resequenced the 18S rDNA of over 20 taxa, and have found that some published sequences are in error by as many as 33 bases, which corresponds to 1.8% of the total gene. In several instances, we discovered numerous errors in the 18S rDNA sequence for a taxon using the same DNA originally used to produce the reported sequence. These errors in previously generated sequences are not confined to base composition, but also involve the presence of what we refer to here as "false" insertions and deletions. For example, we resequenced 18S rDNA from *Zea mays* and discovered that the original sequence included a large number of "false" insertions relative to all other angiosperms. Integrating our new sequence for *Zea* into the angiosperm data matrix and removal of the previously published sequence resulted in the elimination of 14 indels from our 18S rDNA data set, four of which were alignment gaps that had to be added to all other angiosperms. We were able to remove additional alignment gaps through the resequencing of other taxa for which 18S rDNA sequences were reported previously. As a point of comparison, the total length of the aligned sequences in the data matrix of Nickrent and Soltis (1995) for 64 taxa was 1853 bp. In contrast, the length of the aligned sequences in our 228-taxon data matrix is only 1850 bp. The resequencing of additional taxa for which published sequences cause numerous alignment gaps would likely decrease further the total length of the aligned sequences.

The numerous erroneous 18S rDNA sequences in the literature perhaps result from inherent difficulties in sequencing rDNA. Secondary structure in the rRNA for which this gene codes is also pres-

Table 3. Area initially thought to be prone to insertion and deletion; however apparent gaps result from sequencing difficulties. The underlined portion of the *Hydrangea* sequence shows the actual base composition that we have determined to be present for many taxa for this area.

	215 *
Hydrangea	AAAGGTTGACGCGGGCTTTGCCC
Glycine	AAAGGTCAACACAGGCTCTGCCT
Heuchera	AAAGGCCAAC----GCTTTGCCC
Lepuropetalon	AAAGGTCAACGCTTGCTTCGGCT
Prunus	AAAGGCCAAC----GCTCTGCCC
Francoa	AAAGGTCGAC----GCTTTGCCC
Podophyllum	AAAGGTCAACG---GCTTTGCCC
Austrobaileya	AAAGGCCGAT--CGGCTCTGCCC
Caulophyllum	AAAGGTCAAC???????CTGCCC
Buxus	AAAGGTCGA---------TGCC-

ent in the gene itself and may lead to compressions and associated sequencing problems. More than one molecular systematist with substantial experience in the sequencing of chloroplast genes such as *rbc*L has referred to the sequencing of 18S rDNA as "tricky." We have found that preparation of samples via cycle sequencing followed by automated sequencing yields reliable 18S rDNA sequences that appear more accurate than most manually generated sequences. The critical procedural step is likely the cycle sequencing reactions, in which secondary structure is reduced or eliminated by high temperature. Several specific regions of 18S rDNA are particularly difficult to sequence. These include base positions 215–230, 1355–1365, and 1705–1715 (all positions mentioned in this paper correspond to those of *Glycine max*; Eckenrode et al., 1985), as well as several of those small regions noted earlier that are prone to insertion and deletion (positions 230–237; 496–501; 666–672; 1363–1369) (see Appendix).

We will use the first of these regions (base positions 215–230) to illustrate the errors that can result in 18S rDNA sequencing. Based on manual sequences (generated by D. Soltis & R. Kuzoff), the base composition of this region in Saxifragaceae and several other rosid families initially appeared to involve a large deletion relative to some other available sequences (see Table 3). Similarly, the 18S rDNA sequences generated manually by other investigators, representing a diversity of angiosperms, typically were lacking one or more base pairs in this region. Alternatively, researchers scored this region as uncertain, using either "?" or "N." Thus, sequences available prior to this study suggested that this region was highly prone to insertion and deletion. As a result, alignment of this region was initially difficult. Alignment problems were exacerbated by the apparent occurrence of base substitution in the region. Further compounding the difficulty of alignment is the fact that the region just 3′ of this area actually is prone to insertion-deletion, as well as to considerable variation in primary sequence. Base positions 230–237 correspond to one of the variable helix termini noted above. Cycle and automated sequencing of over 100 taxa, however, revealed no indels in the area of positions 215–230. In fact, after resequencing this region in many taxa for which manual sequences initially suggested the presence of numerous indels, we have concluded that indels in this region are either extremely rare or nonexistent. This region is G-C rich; as a result, sequencing "stops" often occurred, yielding only a portion of the base pairs actually present in the region. Alignment of these incomplete sequences suggested numerous indels in this region, leading to the misconception that indels were frequent. Similar sequencing problems were encountered in other portions of the 18S rRNA gene. Taken together, these regions had contributed to the view that insertion and deletion are common in 18S rDNA.

Although the frequency of indels has been overstated for the 18S gene, several regions of 18S rDNA are, in fact, prone to variation in primary sequence and length. However, these regions are small, easily located, and, as noted by Nickrent and Soltis (1995), typically confined to the termini of helices on the proposed secondary structure model for 18S rRNA (e.g., Nickrent & Soltis, 1995). Four such regions, represented by base positions 230–237, 496–501, 666–672, and 1363–1369, correspond to the termini of helices E10-1, 17, E23-1, and 43, respectively (see Appendix). These regions are difficult to align over a broad taxonomic scale, such as all angiosperms, and were therefore not used in our phylogenetic analyses (see Materials and Methods above). On a lower taxonomic scale (e.g., closely related families), however, even these highly variable regions are easily aligned, permitting the use of these regions in more focused studies (e.g., Polemoniaceae and related Asteridae s.l., Johnson et al., unpublished; portions of Saxifragaceae s.l., D. Soltis & Soltis, 1997; Orchidaceae, Cameron & Chase, unpublished).

Because indels in 18S rDNA are neither as prevalent nor as problematic as previously thought, alignment of clean 18S rDNA sequences is straightforward. With the exclusion of the few small regions noted above, alignment of over 200 angiosperm sequences was straightforward and easily accom-

plished by eye. This is also true for the alignment of 18S rDNA sequences on a broader scale across vascular plants (P. Soltis et al., unpublished). As noted above, the resequencing of some taxa greatly facilitated the alignment process in angiosperms.

PHYLOGENETICALLY INFORMATIVE INDELS

Not only do indels in angiosperm 18S rDNA sequences not cause alignment problems, but some indels may be phylogenetically informative at the level of our investigation. Here we do not consider those indels located within the variable regions noted above, but only those indels located in highly conserved regions not normally prone to changes in length. Two such indels in particular (Table 2) appear to be phylogenetically informative across the angiosperms.

One indel involves an apparent deletion of one base pair that unites all higher eudicots (Table 2, indel A). This base pair is present in Gnetales, monocots, paleoherbs, Magnoliales, Laurales, ranunculids, Trochodendraceae, Tetracentraceae, Proteaceae, Sabiaceae, Platanaceae, and Nelumbonaceae and is absent from all higher dicots (i.e., the large Rosidae clade and Asteridae s.l.). Thus, the distribution of this indel agrees with the results of phylogenetic analyses based only on base substitutions (Figs. 1, 2, 4; all figures, plus Appendix, follow Lit. Cit.). In addition, the distribution of this indel also agrees with topologies based on analyses of *rbc*L sequences. It appears, however, that this base pair may also have been lost independently in two of the monocots analyzed here (i.e., *Calla* and *Chlorophytum*).

The second phylogenetically informative indel involves an apparent insertion (Table 2, indel B) that unites all members of the saxifragoid clade (Saxifragaceae s. str. and close allies; this is the Saxifragales of D. Soltis & Soltis, 1997). The saxifragoid clade also is united by base substitutions and represents one of the most strongly supported clades resulting from the phylogenetic analyses.

Additional examples of potentially informative indels can be found at lower taxonomic levels. For example, in Zingiberales, two insertions, each of a single base pair, are found at positions 117 and 260 in all members of the Zingiberaceae (Kress et al., 1995). None of the other approximately 70 monocots for which 18S rDNA has been sequenced exhibits these insertions. Similarly, an insertion of one base at position 655 appears to unite members of Viscaceae.

Undoubtedly, additional 18S rDNA sequencing will reveal more examples of phylogenetically informative indels. However, the discovery of such indels depends on the availability of a large database of accurate sequences. Previously published sequences containing errors and ambiguities, "false" indels, and incompletely sequenced regions have made assessment of the phylogenetic potential of indels in 18S rDNA impossible.

STEM VERSUS LOOP CHANGES/COMPENSATORY CHANGES

The secondary structure of the 18S rRNA transcript may have significant implications for phylogeny reconstruction using rRNA or rDNA sequences (e.g., Mishler et al., 1988; Dixon & Hillis, 1993). The question remains as to whether both loop bases (non-pairing bases) and stem bases (pairing bases) should be used in phylogeny reconstruction and, if so, whether bases from stems and loops should be considered equally informative and independent. Assuming near-perfect compensatory mutation (substitutions that maintain or restore stem base complementarity—e.g., Noller, 1984; Curtiss & Vournakis, 1984; Wheeler & Honeycutt, 1988) in stem regions to maintain secondary structure of the 18S or 26S (28S) rRNA, Wheeler and Honeycutt (1988) recommended that stem bases either be eliminated from phylogenetic analysis or weighted by one-half relative to loop bases. However, in their analyses of 28S rRNA sequences from vertebrates, Dixon and Hillis (1993) found that characters from both stems and loops contain phylogenetic information. They also found that the number of compensatory mutations in stem bases was less than 40% of that expected under a hypothesis of perfect compensation to maintain secondary structure. Dixon and Hillis therefore suggested that the weighting of stem characters be reduced by no more than 20% relative to loop characters in phylogenetic analyses.

The large database of 18S rDNA sequences reported here affords the opportunity to address these and other issues regarding the impact of the secondary structure of the 18S rRNA transcript on phylogeny reconstruction in angiosperms. Although it is not our goal to examine such issues in detail here, we will provide some initial observations regarding the relative importance of both stem and loop mutations and the prevalence of compensatory mutations.

We followed the definitions of stem and loop bases used elsewhere (e.g., Dixon & Hillis, 1993): stem bases are those that participate in base-pairing interactions; loop bases do not engage in base pairing in the mature rRNA. Mapping base substitutions on the proposed 18S rRNA secondary struc-

ture for *Glycine max* (see Appendix), we examined 120 positions (in 60 taxa) at which phylogenetically informative base substitutions had occurred (based on the results of the searches; discussed below). Emphasis was placed on those substitutions that provided synapomorphies for those clades that appear in all shortest trees and that represent several different taxonomic levels (e.g., Asteridae s.l., Caryophyllidae s.l., monocots, glucosinolates, santaloids, Caryophyllales, saxifragoids, celastroids, *Parnassia–Lepuropetalon*). Of these 120 positions, 70 (58%) were stem bases, and 50 (42%) were loop bases. Although this initial survey considers only a subset of synapomorphous base substitutions, it suggests that both stem and loop regions appear to contain phylogenetic information, with perhaps a somewhat greater proportion of informative sites found in stem, rather than loop, regions. This topic certainly requires a more rigorous examination. The relative information content of stem versus loop bases may, in fact, vary at different taxonomic levels. For example, some of the more variable loop regions (several of which were removed from these phylogenetic analyses because the sequences were difficult to align) may hold relatively more information at lower levels (among and within closely related families) than at higher taxonomic levels (ordinal and above), at which the sequences become too divergent for confident alignment.

The frequency of compensatory changes was examined in 21 stem regions located throughout the 18S rRNA gene. Following the general approach of others (e.g., Dixon & Hillis, 1993), we considered two classes of substitutions within stem regions. The first class involves substitutions that change one pair of complementary bases to another pair of complementary bases. This includes "double compensatory" substitutions in which one pair of complementary bases is converted to another (e.g., C-G to A-U). This class also includes changes that require only a single substitution event. That is, because uracil can pair with guanine as well as with adenine, it is possible to have a single change from one base-pairing couplet to another (e.g., U-G to C-G; U-A to U-G). The latter represent one type of "single compensatory" substitutions (sensu Dixon & Hillis, 1993). The second class of stem substitutions involves those that change one pair of complementary bases to a pair of noncomplementary bases, or vice versa (e.g., C-G to G-G; or C-C to C-G). For example, a change of C-G to G-G destroys a base-pairing couplet. Conversely, a change from C-C to C-G creates a base-pairing couplet and represents another example of a "single compensatory" substitution. Of the 216 stem changes we analyzed, 19% were "double compensatory"; 46% were single base substitutions involving uracil that changed one base-pairing couplet to another ("single compensatory"); 8% changed a pair of noncomplementary bases to complementary (the second type of "single compensatory" change); 27% destroyed a base-pairing couplet. Of these changes that result in mispairing of nucleotides, over one-third are adjacent to loop regions. Hence, the loop regions may simply be expanded in these instances. Nearly three quarters (73%) of the stem mutations we analyzed maintain or restore base pairing and would be considered compensatory. In their comparable analysis of 28 rRNA sequences, Dixon and Hillis (1993) observed that only 47% of the mutations maintained or restored base pairing. Our results are more similar to observations for 5S rRNA (Curtiss & Vournakis, 1984), where approximately 88% of the base substitutions analyzed from stem regions were compensatory.

A similar pattern of molecular evolution is seen for 18S rDNA within a single family, Polemoniaceae, and its closest relatives (Johnson et al., unpublished), where 228 variable nucleotide positions were examined. Although most of these 228 positions are located on stems (133 compared to 95 loop characters), the average number of substitutions per site over the potentially informative characters is greater for the loop characters (5.0) than for the stem characters (3.1). Using one of the most parsimonious trees as a framework, Johnson et al. (unpublished) also considered in more detail 67 substitutions that either unite or appear within Polemoniaceae. Of these substitutions, 36 (53.7%) occur in loops. Considering just the 31 stem substitutions, 23 (74.2%) either maintain or restore base-pairing. The remaining eight stem substitutions (25.8%) result in mispairing of nucleotides, with four sites located adjacent to loops.

These initial studies of the relative information content of stem and loop regions and the frequency of compensatory changes have implications for the use and relative weighting of stem and loop bases in phylogeny reconstruction. These data reinforce the findings of others (e.g., Dixon & Hillis, 1993; Smith, 1989) that both stem and loop regions provide important information for phylogeny reconstruction. In addition, the high frequency of observed compensatory change in angiosperm 18S rDNA suggests that perhaps stem characters should receive less weight than loop characters in future analyses. However, weighting of stem versus loop characters is more complex than it might seem initially. Recent work with 18S rDNA sequences in Polemoniaceae (Johnson et al., unpublished) dem-

onstrates that loop regions evolve more rapidly than do stem regions. Thus, in more focused studies in which it is possible to align and use the entire 18S rDNA sequence, stem and loop regions should perhaps be given equal weight. In broader studies in which the rapidly evolving loops are removed due to alignment difficulties and only the more conserved loop regions are included in the analysis, stems should be downweighted; however, more detailed analyses are required to estimate appropriate weights.

II. PHYLOGENETIC RELATIONSHIPS

Each broad phylogenetic analysis yielded thousands of most parsimonious trees; it is likely that shorter trees exist for all four data sets and that additional classes of most-parsimonious trees were not recovered. Nonetheless, we feel that it is significant that analyses of three of the four data sets suggest the same general topology. The shortest trees obtained from searches of data sets 1 and 2 are essentially identical, and differences between the shortest trees from analysis of these two data sets and data set 4 are minor and weakly supported. Although phylogenetic analysis of data set 3 revealed many of the same major clades recovered by searches of the other data sets, relationships among some of these clades differ; most notable are the weakly supported, unusual positions of monocots and saxifragoids (see below).

All searches revealed the same major clades (e.g., Rosidae, Asteridae s.l., Caryophyllidae s.l., monocots, saxifragoids), as well as the same suite of taxa as sister to all remaining angiosperms. In general, the trees obtained in these exploratory, broad analyses of 18S rDNA sequences depict relationships very similar to those obtained in broad analyses of *rbc*L sequences (Chase et al., 1993). The general features observed in the shortest trees obtained from the four searches are discussed below. The several unusual relationships among major clades suggested by analyses of data set 3 are discussed in more detail below under "Differences Among the Shortest Trees."

FIRST-BRANCHING FAMILIES

Phylogenetic analyses of three of four data sets (data sets 1, 2, and 4) suggest that those taxa having uniaperturate pollen (monosulcate and monosulcate-derived) and ethereal oils appear as early-branching angiosperms, forming a grade (labeled monosulcate grade in Figs. 1, 2, and 4). Those plants having triaperturate pollen (tricolpate and tricolpate-derived), with a few exceptions (see below), and tannins and alkaloids as secondary compounds form a clade (labeled eudicot clade). The latter group has been referred to as the eudicots (Donoghue & Doyle, 1989b; Doyle & Hotton, 1991; Chase et al., 1993). Although the term eudicot has been variously defined, we will use the Chase et al. (1993) definition to facilitate comparison between the two studies. A eudicot clade was also recovered in analyses of *rbc*L sequences (Chase et al., 1993), but, instead of forming a grade, as they do here, those plants with uniaperturate pollen form a weakly supported clade in the *rbc*L trees.

There are two major exceptions to the general correspondence between the eudicot clade and the distribution of the triaperturate pollen types (other than the obvious departures observed in the trees derived from analysis of data set 3). First, the Winteraceae and several families of paleoherbs (Chloranthaceae, Lactoridaceae, Aristolochiaceae) all possess uniaperturate pollen, yet appear within the eudicot (triaperturate) clade in the shortest trees obtained in analyses of data sets 1 and 2 (Figs. 1, 2). These exceptions may reflect low taxon density and/or the low resolving power of 18S rDNA sequence data (see below); these taxa seem to be unstable in position in the various searches. In broad analyses of *rbc*L sequences, in contrast, these taxa are clearly members of the uniaperturate clade.

The second exception involves Illiciaceae and Schisandraceae. Unlike the examples above, however, which we suspect represent spurious phylogenetic placements, Illiciaceae and Schisandraceae appear to be true early-branching angiosperms (see below), yet possess triaperturate pollen. These families similarly appear as early-branching angiosperms in analyses based on *rbc*L sequences (Chase et al., 1993; Qiu et al., 1993). As reviewed by Doyle et al. (1990), however, the tricolpate condition in Illiciaceae and Schisandraceae is different from that which characterizes eudicots. Hence, the 18S rDNA analyses further support the *rbc*L-based inferences of Qiu et al. (1993) that Illiciaceae and Schisandraceae represent an independent evolution of tricolpate pollen.

Four families of woody Magnoliidae consistently appear as sister taxa to all remaining angiosperms analyzed: Amborellaceae and a clade of Austrobaileyaceae, Illiciaceae, and Schisandraceae. The latter three families form one of the most strongly supported clades in this study (jackknife value of 94%). In searches of data sets 1 and 2, a clade of Austrobaileyaceae, Illiciaceae, and Schisandraceae is the sister group to all other angiosperms, followed subsequently by Amborellaceae; in analyses of data sets 3 and 4, the positions of these two

lineages are reversed. Surprisingly, given the close relationship suggested between Illiciaceae and Schisandraceae by others (e.g., Cronquist, 1981; Qiu et al., 1993), *Illicium* is sister to *Austrobaileya-Schisandra* in all four analyses. These four genera, with Nymphaeales, form a clade in the *rbc*L analyses of Chase et al. (1993) and Qiu et al. (1993).

In the shortest trees resulting from searches of all four data sets, from one to several families of paleoherbs (sensu Donoghue & Doyle, 1989a) subsequently follow Austrobaileyaceae, Illiciaceae, Schisandraceae, and Amborellaceae. Nymphaeaceae immediately follow these four families in all shortest trees. In searches of data sets 1 and 2, Nymphaeaceae form a clade with Piperaceae and Saururaceae (represented by *Peperomia* and *Houttuynia* and *Saururus*, respectively; jackknife value of 85%), whereas in searches of data set 4, these same three families form a grade with Nymphaeaceae as sister to all remaining angiosperms, followed by a clade of Piperaceae and Saururaceae. In searches of data set 3, Nymphaeaceae also follow Austrobaileyaceae, Illiciaceae, Schisandraceae, and Amborellaceae, but Nymphaeaceae are then followed by saxifragoids, an unusual placement discussed in more detail below.

Amborellaceae, followed by (1) a clade of Austrobaileyaceae, Illiciaceae, and Schisandraceae, (2) Nymphaeaceae, (3) a clade or grade of Piperaceae, Saururaceae, Aristolochiaceae, and Lactoridaceae (similar to Fig. 4), appear as the first-branching angiosperms when *Zamia* and *Cycas* are used as additional outgroups (see Materials and Methods). In preliminary analyses of a larger data set of 271 angiosperms using species of *Welwitschia, Gnetum,* and *Ephedra* as outgroups, Amborellaceae, a clade of Austrobaileyaceae–Illiciaceae–Schisandraceae, and Nymphaeaceae again appear as successive sisters to all remaining angiosperms.

The position of woody magnoliids as first-branching taxa in these 18S rDNA trees is in general agreement with traditional views of angiosperm relationships (e.g., Cronquist, 1968, 1981; Stebbins, 1974; Takhtajan, 1969, 1980) that suggest that woody Magnoliidae are the most primitive extant angiosperms. The morphological analyses of Donoghue and Doyle (1989a) and Loconte and Stevenson (1991) also support the woody Magnoliidae as the most ancestral living group of angiosperms. Other data also point to the antiquity of at least some of these genera. For example, Endress and Honegger (1980) determined that the pollen of *Austrobaileya* resembles *Clavatipollenites,* one of the oldest probable angiosperm fossils, and concluded that *Austrobaileya* may be "especially archaic among the angiosperms." If the 18S rDNA inference is correct in suggesting that Amborellaceae, a family lacking vessel elements, are among the first-branching angiosperms, this analysis may support the hypothesis that the angiosperms were primitively vesselless (Bailey, 1957; Cronquist, 1981; Young, 1981).

In contrast to this study, analyses based on partial 18S and 26S rRNA sequences suggested that a group of paleoherbs (Aristolochiales, Piperales, Nymphaeales) is the sister taxon to all other flowering plants (Hamby & Zimmer, 1992). However, of the four woody families of Magnoliidae appearing as first-branching taxa in our 18S rDNA trees (Amborellaceae, Schisandraceae, Illiciaceae, and Austrobaileyaceae), only Illiciaceae were sampled by Hamby and Zimmer (1992). Other phylogenetic analyses similarly support the position of some paleoherbs as first-branching taxa among the angiosperms (e.g., Doyle et al., 1994; Nixon et al., 1994). Paleoherbs are sister to other angiosperms in trees based on a combination of morphology and rRNA sequence data and in those derived independently from morphological and rRNA data (Doyle et al., 1994). However, this topology is only weakly supported by morphological data, with trees rooted next to Magnoliales only one step longer. Furthermore, the rRNA data set employed by Doyle et al. (1994) is that of Hamby and Zimmer (1992), which, as noted above, lacked several critical woody magnoliids.

Broad phylogenetic analyses of *rbc*L sequences (Chase et al., 1993; Rice et al., 1997) place the aquatic genus *Ceratophyllum* as sister to all remaining angiosperms. This placement of *Ceratophyllum* also has been suggested on morphological grounds (Les, 1988; Les et al., 1991; Nixon et al., 1994), although alternative trees in the latter study place the paleoherb family Chloranthaceae as sister to the remaining flowering plants. A number of floral features of *Ceratophyllum* also conform to the view that the genus represents a primitive angiosperm (Endress, 1994). However, *Ceratophyllum* does not appear as first-branching in any of our phylogenetic analyses. Searches involving three of the four data sets (1, 2, and 4) place *Ceratophyllum* as sister to the monocots, a finding in general agreement with earlier rRNA sequence analyses (Hamby & Zimmer, 1992).

Subsequent to the Amborellaceae, Austrobaileyaceae, Illiciaceae, Schisandraceae, Nymphaeaceae, and Piperales, in analyses of three of four data sets (1, 2, and 4) are additional families and orders of Magnoliidae: Annonaceae, Calycanthaceae, and

Lauraceae, all woody families traditionally considered among the most primitive extant angiosperms.

With the exception of the shortest trees resulting from analysis of data set 3, the monocots also appear as an early lineage of angiosperms. The monocots are monophyletic, with the exception of *Acorus*, which does not appear closely related to the other member of Araceae included (*Calla*). In analyses of the two data sets (1 and 2) that included *Acorus*, *Acorus* follows Nymphaeaceae–Piperales as the subsequent sister to all remaining angiosperms. In analyses of *rbc*L sequences, *Acorus* was considered "phylogenetically isolated" as sister to the remaining monocots (Duvall et al., 1993). Phylogenetic results based on 18S rDNA sequences also suggest that *Acorus* is anomalous among monocots. Given its long branch length and unexpected position, the 18S rDNA of *Acorus* should be resequenced, and additional monocots should be added to the data set before the affinities of this enigmatic genus are addressed further.

Because our sampling of monocots was limited, to permit more thorough treatment elsewhere, relationships within the monocots will not be discussed here in any detail. Nonetheless, several traditionally recognized groups of monocots appear to be monophyletic, including Zingiberales, Liliales, and higher commelinoids. Furthermore, the bromeliads are grouped with the grasses and allies, as expected (Duvall et al., 1993). The two best supported clades within the monocots are Zingiberales (*Maranta, Zingiber, Costus, Canna, Heliconia,* and *Musa;* jackknife value of 58%) and a clade composed of Sparganiaceae, Cyperaceae, Poaceae, and Bromeliaceae (*Sparganium, Cyperus, Oryza, Zea,* and *Glomeropitcairnia*; jackknife value of 59%). Surprising results, given *rbc*L topologies (Duvall et al., 1993) and morphological features, include the placement of Orchidaceae (*Oncidium*) as the sister, or one of the sisters, to the remaining monocots and the placement of Arecaceae (*Veitchia*) and Alismataceae (*Sagittaria*) within the Asparagales (Figs. 1, 2). These unusual placements should not be considered seriously, however, due to the low representation of the monocots.

EUDICOT CLADE

Analyses of three of four data sets (1, 2, and 4) clearly reveal a eudicot (or triaperturate) clade (Figs. 1, 2, 4), with the following successive sister groups at its base (Figs. 1, 2): Proteaceae, Nelumbonaceae, Platanaceae, a clade of ranunculids, Trochodendraceae/Tetracentraceae, and a clade composed of Winteraceae (*Drimys*), Aristolochiaceae (*Aristolochia, Asarum, Saruma*), Lactoridaceae, Sabiaceae, and Chloranthaceae (*Hedyosmum*). The latter clade is an unexpected grouping (see below) of paleoherbs (Aristolochiaceae, Lactoridaceae, Chloranthaceae), woody Magnoliales (Winteraceae), and eudicots (Sabiaceae). With the exception of Aristolochiaceae, Lactoridaceae, Chloranthaceae, and Winteraceae, the presence of the remaining taxa on branches at the base of the eudicots closely parallels results retrieved from the phylogenetic analyses of *rbc*L sequences (Chase et al., 1993).

In the shortest trees obtained in analyses of data set 4, the distinction between the monosulcate grade and the eudicot clade is less clear than in the shortest trees obtained from the analyses of data sets 1 and 2 (see "Lower Eudicots/Monosulcates," Fig. 4). Platanaceae, Trochodendraceae/Tetracentraceae, ranunculids (which are paraphyletic), Proteaceae (*Knightia*), Buxaceae, Sabiaceae, and a clade of Chloranthaceae (*Hedyosmum*)/Winteraceae (*Drimys*) again appear as sister groups to the remainder of the eudicot clade. Also in this same lower eudicot/monosulcate grade, however, are Calycanthaceae, Annonaceae (*Mkilua*), and Lauraceae (*Sassafras*), uniaperturate families that appear in a clade with some ranunculids (Fig. 4).

In the shortest trees obtained in analyses of all data sets, the remainder of the eudicot clade is essentially composed of two large subclades, one consisting largely of Rosidae plus some Dilleniidae and the other corresponding to the Asteridae s.l. (labeled Rosidae and Asteridae s.l., respectively, in Figs. 1, 2, 4). With a few exceptions, most notably the placement of the monocots within the Rosidae clade, these two large clades also are present in the trees derived from searches of data set 3. The Rosidae and Asteridae s.l. clades were also recovered in broad analyses of *rbc*L sequences (Chase et al., 1993; Olmstead et al., 1992, 1993; Rice et al., submitted), although the placement of Caryophyllidae s.l. is very different in the 18S rDNA and *rbc*L topologies (see below). These two large clades, Rosidae and Asteridae s.l., reflect the basic division of higher dicots into two major groups (Young & Watson, 1970), with (1) polypetalous corollas and nontenuinucellate ovules and (2) sympetalous corollas and tenuinucellate ovules, respectively. Below we discuss in more detail the major clades of eudicots based on phylogenetic analyses of 18S rDNA sequences. We use informal names in most instances to refer to strongly supported clades (e.g., celastroids, saxifragoids, ranunculids), some of which differ dramatically from traditional views of rela-

tionship, but formal taxonomic change may be warranted for many of these.

Ranunculids. The searches of the larger data sets (Figs. 1, 2) recovered a clade (labeled "Ranunculids") containing Lardizabalaceae, Berberidaceae, Ranunculaceae, Menispermaceae, Eupteleaceae, Fumariaceae, Sargentodoxaceae, and Papaveraceae. This same clade was found in the broad analyses of *rbc*L sequences (Chase et al., 1993); it represents the core of the Ranunculales (sensu Cronquist, 1981) and corresponds closely to the Berberidales of Thorne (1992) and the Ranunculiflorae of Dahlgren (1980). Analyses of not only *rbc*L and 18S rDNA sequences, but also *atp*B sequences, place Eupteleaceae (Hamamelidae) within this clade (Hoot & Crane, 1995). Also part of this clade in the 18S rDNA analyses is Sargentodoxaceae, a family typically placed in Ranunculales and allied with Lardizabalaceae (e.g., Cronquist, 1981). In contrast, analyses of *rbc*L sequences placed Sargentodoxaceae with Fabaceae (Chase et al., 1993). This result is due to the misidentification of leaf material in the *rbc*L analysis (Qiu, pers. comm.). Reanalysis of *Sargentodoxa* for *rbc*L places it as sister to the Lardizabalaceae (Hoot & Crane, 1995; Hoot et al., 1995).

Searches involving the two small data sets (3 and 4) employed fewer representatives of Ranunculales. In trees resulting from searches of data set 4, these taxa form a grade as some of the early-branching eudicots. In trees from searches of data set 3, in contrast, the ranunculids appear polyphyletic. The placements of the ranunculids in analyses of data sets 3 and 4 may well reflect their decreased representation (lower taxon density) in these searches. In preliminary analyses of a 271-taxon 18S rDNA data set including more ranunculids, the ranunculids again form a monophyletic group.

Saxifragoids. All analyses of 18S rDNA sequences (Figs. 1–4) reveal a clade composed of *Heuchera, Boykinia, Saxifraga* (Saxifragaceae s. str.), *Crassula, Sedum, Dudleya,* and *Kalanchoe* (Crassulaceae), *Pterostemon, Tetracarpaea, Ribes,* and *Itea* (Grossulariaceae), *Penthorum* (placed in Saxifragaceae by Cronquist, 1981), *Altingia* and *Liquidambar* (Hamamelidaceae), Haloragaceae, Cercidiphyllaceae, Daphniphyllaceae, and Paeoniaceae; this clade is referred to here as saxifragoids. This clade is one of the most strongly supported findings of this investigation (jackknife value of 68%). The same saxifragoid clade (also referred to as Saxifragales) was identified in an analysis of 130 18S rDNA sequences aimed at elucidating the affinities of the morphologically diverse members of Saxifragaceae s.l. (D. Soltis & Soltis, 1997). The monophyly of this clade is supported not only by base substitutions, but also by the presence of an insertion (see Table 2) located in a portion of the 18S rRNA gene that is highly conserved in length. An identical clade (referred to as rosid III) is revealed in the 499-taxon analysis of *rbc*L sequences (Chase et al., 1993) and is also retrieved in preliminary analyses of a 271-taxon 18S rDNA data set including more Hamamelidaceae, as well as in phylogenetic analyses involving *mat*K sequences (Hibsch-Jetter & Soltis, unpublished) and preliminary work with *atp*B sequences (Hoot, unpublished). As reviewed in more detail by D. Soltis and Soltis (1997), this small clade is noteworthy in that it contains taxa traditionally placed in three subclasses: Paeoniaceae (Dilleniidae); Hamamelidaceae, Daphniphyllaceae, Cercidiphyllaceae (Hamamelidae); the remaining taxa are all members of Rosidae.

Although this saxifragoid clade is recovered by analyses of both 18S rDNA and *rbc*L sequences, this same group of taxa has never been recognized in any classification. Whereas Saxifragaceae s. str., *Ribes, Itea, Tetracarpaea, Pterostemon, Penthorum,* and Crassulaceae are considered closely related members of Rosidae in virtually all recent treatments (e.g., Cronquist, 1981; Thorne, 1992; Takhtajan, 1987; Dahlgren, 1980, 1983), the affinities of the rosid family Haloragaceae and the dilleniid family Paeoniaceae have been considered enigmatic (e.g., Cronquist, 1981). The hamamelid families found in this clade (Hamamelidaceae, Cercidiphyllaceae, and Daphniphyllaceae) typically have not been considered close relatives of Saxifragaceae s. str. and allied rosids. The relationships of these more anomalous members of this clade are discussed in more detail by D. Soltis and Soltis (1977).

Glucosinolate clade. Another clade revealed by all analyses (Figs. 1–4) comprises glucosinolate-producing taxa. The families that compose this clade in Figures 1–4 are 7 of the 15 families known to produce glucosinolates (mustard oil glucosides): Limnanthaceae, Brassicaceae, Capparaceae, Moringaceae, Caricaceae, Bataceae, and Tropaeolaceae. Whereas Brassicaceae and Capparaceae have long been recognized as closely related, the remaining families included in this study (Limnanthaceae, Moringaceae, Caricaceae, Bataceae, and Tropaeolaceae) are morphologically diverse and have been placed in distinct orders (e.g., Cronquist, 1981; see review by Rodman et al., 1993). The genus *Drypetes* (Euphorbiaceae) also produces glucosinolates, but it does not appear to be closely

related to the glucosinolate clade in any of the four searches. Phylogenetic analyses of 18S rDNA sequences involving additional glucosinolate taxa further demonstrate the monophyly of the glucosinolate-producers, with the exception of *Drypetes*, and also clarify relationships among the members of this clade (Rodman et al., submitted). These results closely parallel findings based on the phylogenetic analysis of *rbc*L sequences (Rodman et al., 1993; Chase et al., 1993) and morphology (Rodman, 1991). Thus, both *rbc*L and 18S rDNA sequence data indicate that there were two independent origins of the mustard oil syndrome (see Rodman et al., 1993, submitted).

Nitrogen-fixing clade. Species of only 10 families of angiosperms are known to form symbiotic associations with nitrogen-fixing bacteria in root nodules (Fabaceae, Betulaceae, Casuarinaceae, Coriariaceae, Datiscaceae, Elaeagnaceae, Myricaceae, Rhamnaceae, Rosaceae, and Ulmaceae). These families are distributed among four of Cronquist's (1981) six subclasses of dicotyledons, implying that many of these families are only distantly related. Recent phylogenetic analyses of *rbc*L sequences reveal, however, that representatives of all ten of these families occur together in a single clade ("nitrogen-fixing clade"; Soltis et al., 1995). In addition to these ten families, this clade also contains several families not known to form associations with nitrogen-fixing bacteria, including Moraceae, Cannabaceae, Urticaceae, Polygalaceae, Fagaceae, Begoniaceae, and Cucurbitaceae.

Analyses of three of four 18S rDNA data sets (Figs. 1, 2, 4) suggest an alliance of taxa similar to that revealed by *rbc*L sequences. This clade in large part represents a subset of the taxa present in the *rbc*L-based nitrogen-fixing clade. The families in the 18S rDNA-based nitrogen-fixing clade include Betulaceae, Casuarinaceae, Datiscaceae, Elaeagnaceae, Rhamnaceae, and Ulmaceae, all families that form symbiotic associations with nitrogen-fixing bacteria. Other families known to form such associations (i.e., Coriariaceae and Myricaceae) and that appeared in the *rbc*L-based nitrogen-fixing clade were not analyzed for 18S rDNA sequence variation. Also part of the nitrogen-fixing clade retrieved here are Begoniaceae, Moraceae, Urticaceae, and Cucurbitaceae, families also found to be part of this alliance based on analyses of *rbc*L sequences. However, neither Rosaceae nor Fabaceae, two families involved in nitrogen-fixing symbioses, are included within the 18S rDNA nitrogen-fixing clade, although both families are part of this alliance in the *rbc*L-based trees (Soltis et al., 1995).

Searches involving the two larger data sets (1 and 2) also place three families of Malvales (Malvaceae, Bombacaceae, and Tiliaceae) within the nitrogen-fixing clade; these taxa were not part of the nitrogen-fixing clade in the *rbc*L-based trees. In analyses of data set 4, however, these three families of Malvales are not part of the nitrogen-fixing clade (Fig. 4). No clear nitrogen-fixing clade emerged in analyses of data set 3; instead, these taxa are part of a grade that represents the first branches of a primarily rosid-dilleniid clade (Fig. 3).

Asteridae sensu lato. Analyses of all four 18S rDNA data sets also reveal an expanded Asteridae clade (Asteridae s.l.) that agrees closely with that recovered by analyses of *rbc*L sequences (Olmstead et al., 1992, 1993; Chase et al., 1993). In addition to the conventionally circumscribed Asteridae, this clade also includes a number of families placed in Dilleniidae, such as Ericaceae, Clethraceae, Pyrolaceae, Styracaceae, Ebenaceae, Actinidiaceae, Sarraceniaceae, Fouquieriaceae, Theaceae, and Primulaceae. Also present in Asteridae s.l. are Nyssaceae, Pittosporaceae, Apiaceae, Araliaceae, and Hydrangeaceae, all members of Rosidae. In addition, Eucommiaceae, a member of Hamamelidae, and *Byblis*, a genus of carnivorous plants usually placed in Rosidae, also appear within Asteridae s.l. All analyses also place an expanded Caryophyllidae (Caryophyllidae s.l.) within the Asteridae s.l. clade, an unexpected result that is discussed in more detail below.

Within Asteridae s.l., several subclades or grades can be identified that agree, in large part, with some of the groups identified in analyses of *rbc*L sequences (Chase et al., 1993; Olmstead et al., 1993). Perhaps most noteworthy of these is the ericalean grade (the asterid III clade of Chase et al., 1993) observed in all of the shortest 18S rDNA trees (Figs. 1–4). Other clades of Olmstead et al. are also observed to be monophyletic, including Dipsacales, Boraginales, Gentianales, Asterales s.l., and Lamiidae. Additional asterid taxa should be sequenced for 18S rDNA to assess more rigorously the monophyly of these groups and their interrelationships.

Caryophyllidae sensu lato. All analyses of 18S rDNA sequences reveal a clade composed of Nyctaginaceae (*Mirabilis*), Chenopodiaceae (*Spinacia*), Phytolaccaceae (*Phytolacca*), Aizoaceae (*Tetragonia*), and Molluginaceae (*Mollugo*). These five families represent Caryophyllales (e.g., Cronquist, 1981), the monophyly of which is supported in this study by a jackknife value of 58%, as well as by numerous lines of morphological and molecular

data (e.g., Rodman et al., 1984; Rettig et al., 1992). Sister to this clade of Caryophyllales is another strongly supported clade comprising Plumbaginaceae and Polygonaceae (jackknife value of 77%): this group collectively represents Caryophyllidae (sensu Cronquist, 1981). The monophyly of Caryophyllidae is only weakly supported by cladistic analysis of morphological, chemical, anatomical, and palynological features (Rodman et al., 1984). Analyses of 18S rDNA sequences also suggest that two families of carnivorous plants, Droseraceae and Nepenthaceae, are sister to Caryophyllidae, and we refer to this entire assemblage as Caryophyllidae s.l. (Figs. 1–4).

Phylogenetic analyses of *rbc*L sequences similarly recovered a Caryophyllidae s.l. clade composed of Caryophyllales, Polygonaceae, Plumbaginaceae, Droseraceae, and Nepenthaceae (Chase et al., 1993). One of the broad analyses of *rbc*L sequences (search A, Chase et al., 1993) placed Vitaceae and Dilleniaceae with this expanded Caryophyllidae clade. In the analyses of 18S rDNA sequences, Vitaceae were not sampled, and Dilleniaceae are well removed from Caryophyllidae s.l. The anomalous placement of Dilleniaceae near the monocots (Figs. 1, 2) is discussed below.

Santaloids. Analyses of all four data sets reveal a monophyletic santaloid clade or Santalales, which are represented here by only three families (Opiliaceae, Santalaceae, and Viscaceae). However, in preliminary analyses in which Santalales are represented by seven families (Opiliaceae, Santalaceae, Viscaceae, Eremolepidaceae, Misodendraceae, Loranthaceae, and Olacaceae), santaloids again form a clade. These seven families are widely considered to form a natural group based on morphology (e.g., Cronquist, 1981) and have been shown to form a clade in previous, smaller analyses of 18S rDNA sequences (Nickrent & Franchina, 1990; Nickrent & Soltis, 1995).

Although santaloids appear monophyletic, the position of this clade varies among the analyses. In analyses of data sets 1 and 2, santaloids are sister to *Polygala* and closely related to the legumes. Analysis of data set 4 again places santaloids with *Polygala* and a legume (*Pisum*), as well as with *Gunnera*. Analysis of data set 3 results in an unusual placement of santaloids with several paleoherbs. These findings parallel those of Chase et al. (1993) based on *rbc*L sequences in which the position of santaloids differed greatly between the 476- and 499-taxon searches. In the former, santaloids and *Gunnera* form the asterid V clade; in the latter, santaloids are sister to the caryophyllids, but again appear near *Gunnera*. Thus, whereas both *rbc*L and 18S rDNA searches occasionally place santaloids near *Gunnera*, analyses of three of the four 18S rDNA data sets place santaloids close to Fabaceae and Polygalaceae.

Celastroids. Another small clade revealed in all analyses consists of *Lepuropetalon* and *Parnassia* (Saxifragaceae s.l.), *Brexia* (Grossulariaceae), and *Euonymus* (Celastraceae). This clade, labeled celastroids (Figs. 1–4), was also recovered in analyses of *rbc*L sequences (Chase et al., 1993; Morgan & Soltis, 1993). Although this initially appears to be an eclectic assemblage (*Brexia* is a genus of small trees; *Lepuropetalon spathulatum* is the smallest terrestrial angiosperm), embryological and morphological data also unite these taxa (reviewed in Morgan & Soltis, 1993). The celastroid clade consists of two pairs of genera, each of which is strongly supported: *Lepuropetalon–Parnassia* (jackknife = 100%) and *Brexia–Euonymus* (jackknife = 67%). These same two pairs of genera also were revealed in analyses of *rbc*L sequences (Chase et al., 1993; Morgan & Soltis, 1993).

Cunonioids. *Bauera* and *Ceratopetalum* (Cunoniaceae) and *Eucryphia* (Eucryphiaceae) form a clade with a jackknife value of 53%. A close relationship among these genera also was revealed by a cladistic analysis of morphological features (Hufford & Dickison, 1992). *Bauera, Ceratopetalum,* and *Eucryphia* constitute the core of a very well supported clade (jackknife value of 89%) labeled cunonioids (Figs. 1–4) that also contains Cephalotaceae, a family of carnivorous plants, and *Sloanea* (Elaeocarpaceae). A close relationship of Cephalotaceae to these same representatives of Cunoniaceae and Eucryphiaceae also is suggested by analyses of *rbc*L sequences (Chase et al., 1993; Morgan & Soltis, 1993). *Sloanea* was not represented in the broad analyses of *rbc*L sequences. Other taxa that appear closely allied with Cunoniaceae, Eucryphiaceae, and Cephalotaceae in *rbc*L analyses include Tremandraceae and Oxalidaceae; these families were not included, however, in the 18S rDNA analyses.

Other noteworthy relationships. As recently reviewed (Qiu et al., 1993), the placement of Lactoridaceae has been controversial, with relationships to Magnoliales, Laurales, and Piperales all proposed. Analyses of *rbc*L sequences suggested a close relationship of Lactoridaceae to Aristolochiaceae (Chase et al., 1993), and analyses of 18S rDNA sequences similarly suggest that these two

families are sisters (Figs. 1–4), an inference strongly supported by a jackknife value of 82%.

Additional, small monophyletic groups also merit brief discussion. Bombacaceae, Tiliaceae, and Malvaceae (represented by *Bombax, Luhea,* and *Gossypium,* respectively) form a strongly supported clade (jackknife value of 78%) in all 18S rDNA analyses, in agreement with both traditional treatments (all are members of Malvales) and topologies based on *rbc*L sequences. However, *Sloanea* (Elaeocarpaceae–Malvales) does not appear with Bombacaceae–Tiliaceae–Malvaceae in any of the 18S rDNA trees (Figs. 1–4). As noted above, this malvoid clade sometimes is embedded within the nitrogen-fixing clade (Figs. 1, 2), a placement at odds with analyses based on *rbc*L sequences. This unusual placement could be the result of insufficient taxon density in that many of the closest putative relatives of Malvales were not included here (e.g., Anacardiaceae, Simaroubaceae, Leitneriaceae, Sterculiaceae, Dipterocarpaceae).

On a broader scale, all 18S rDNA topologies suggest that Hamamelidae comprise a number of phylogenetically distinct lineages. For example, Trochodendraceae, Tetracentraceae, and Platanaceae appear near the base of the eudicots in trees derived from searches of data sets 1, 2, and 4 (Figs. 1, 2, 4). Eupteleaceae also appear near the base of the eudicots, but as part of the ranunculid clade. Three traditional families of Hamamelidae, Hamamelidaceae, Cercidiphyllaceae, and Daphniphyllaceae, are part of a well supported saxifragoid clade (Figs. 1–4). Still other families of Hamamelidae (i.e., Betulaceae, Urticaceae, Moraceae, and Ulmaceae) are part of the nitrogen-fixing clade, and Eucommiaceae are nested within the Asteridae s.l. The pronounced polyphyly of Hamamelidae was similarly revealed by analyses of *rbc*L sequences. Both 18S rDNA and *rbc*L sequence data suggest similar placements for representatives of this subclass.

Topologies based on 18S rDNA sequences also reveal the polyphyly of subclass Dilleniidae. Taxa attributed to Dilleniidae appear in several phylogenetically well separated clades. Paeoniaceae appear in the saxifragoid clade, Nepenthaceae and Droseraceae appear in Caryophyllidae s.l., Capparales, Batales, and Violales appear in the glucosinolate clade, and several orders (e.g., Violales, Ebenales, Ericales, Diapensiales, Primulales, and Theales) appear in Asteridae s.l. Other representatives of Dilleniidae (e.g., Turneraceae, Elaeocarpaceae) are scattered throughout the large Rosidae clade.

DIFFERENCES AMONG THE SHORTEST TREES

The shortest trees resulting from analyses of data sets 1 and 2 are essentially identical (Figs. 1, 2) and in turn are very similar to those derived from searches of data set 4 (Fig. 4). The most unusual topology results from searches of data set 3 (Fig. 3). For example, the distinction between the monosulcate grade and the eudicot clade does not occur in the shortest trees from this analysis, with the monocots part of a predominantly rosid assemblage and saxifragoids appearing as one of the early-branching lineages of angiosperms. The ranunculids are not monophyletic in trees from searches of data set 3, with two genera (*Hypecoum* and *Dicentra*) appearing as sister to the monocots and the remaining ranunculids appearing as part of a clade that occupies the unusual position of sister to Asteridae s.l. (see Asteridae s.l. Plus, Fig. 3). However, some of our numerous searches of data set 3 found trees only one step longer than the shortest trees that have a topology essentially identical to that resulting from analysis of the other small data set (4).

Although searches of data sets 1, 2, and 4 yielded similar topologies, several weakly supported differences also exist among the shortest trees found. For example, in trees derived from analyses of data sets 1 and 2, one group of paleoherbs (Aristolochiaceae, Lactoridaceae) appears within the eudicot clade, rather than within the monosulcate grade, as would be expected. In contrast, in trees derived from the smaller data sets (3 and 4), Aristolochiaceae and Lactoridaceae appear within the monosulcate grade, close to other families of paleoherbs (e.g., Piperaceae, Saururaceae). In addition, the shortest trees obtained from analyses of data sets 1 and 2 show a more well defined break between the monosulcate grade and lower eudicots than do trees from data set 4 (compare Figs. 1, 2, and 4). For example, trees resulting from analyses of data set 4 place the monosulcate families Calycanthaceae, Annonaceae, and Lauraceae with Proteaceae (see Fig. 4, Lower eudicots/monosulcates). These and other differences may be the result of insufficient taxon density in certain portions of the tree, incomplete analysis, or lack of signal (see Caveats below).

ANOMALOUS PLACEMENTS

Perhaps the most unusual consistent feature of the 18S rDNA trees involves the placement of Caryophyllidae s.l. within Asteridae s.l. Although Caryophyllidae s.l. form a well supported clade, the position of this clade within Asteridae s.l. is not strongly supported. Some of the many searches con-

ducted retrieved trees only two steps longer than the shortest trees obtained in which Caryophyllidae s.l. are not part of Asteridae s.l., but appear instead within the Rosidae clade. Furthermore, analyses of 130 dicot 18S rDNA sequences aimed at resolving the relationships of Saxifragaceae s.l. did not place the Caryophyllidae s.l. within Asteridae s.l., but instead showed the caryophyllids to be embedded within a rosid clade (D. Soltis & Soltis, 1997). Although the placement of Caryophyllidae s.l. varies in the broad analyses of *rbc*L sequences (Chase et al., 1993), this clade does not appear closely related to the asterids in any of the shortest trees obtained. The 476-taxon analysis places Caryophyllidae s.l. within a clade of rosids, whereas the 499-taxon analysis places them near the split between the clades of higher eudicots (i.e., Rosidae and Asteridae s.l.).

Other anomalous placements include the position in some analyses (Figs. 1, 2) of one group of paleoherbs (Chloranthaceae, Aristolochiaceae, Lactoridaceae) plus Winteraceae of Magnoliales near the base of the eudicot clade. These taxa often are considered to represent early-branching or primitive angiosperms in both analyses of *rbc*L sequences (Chase et al., 1993; Qiu et al., 1993) and recent classification schemes (e.g., Cronquist, 1981; Thorne, 1992; Takhtajan, 1987). Based on phylogenetic analyses of *rbc*L sequences (e.g., Chase et al., 1993; Qiu et al., 1993), for example, Chloranthaceae, Aristolochiaceae, and Lactoridaceae are part of the monosulcate clade. As noted above, however, in some of our searches (see Figs. 3 and 4), Chloranthaceae, Aristolochiaceae, and Lactoridaceae do appear closer to the base of the angiosperms with other monosulcate taxa.

Analyses of data set 4 recovered a clade consisting of *Sagittaria* (Alismataceae) and *Cuscuta* (Cuscutaceae), placed in the Rosidae clade. In trees resulting from analyses of all other data sets, these genera appear with the monocots and Asteridae s.l., respectively, in agreement with traditional views and with trees based on *rbc*L sequences (Chase et al., 1993). The unusual relationship suggested by searches of data set 4 likely results from the more limited taxon sampling of this data set (fewer monocots are included, for example, compared to data sets 1 and 2) and long-branch attraction. *Sagittaria* and *Cuscuta* have very long branches (e.g., 39 and 65 steps, respectively, in Fig. 2) in all of the shortest trees obtained. In analyses of data sets 1 and 2, the long branch of *Cuscuta* also seems to affect the placement of *Ipomoea* (Convolvulaceae), with both appearing in Lamiales instead of Solanales.

The three subfamilies of Fabaceae, Papilionoideae, Mimosoideae, and Caesalpinioideae (represented by *Pisum* and *Glycine*; *Albizia*; *Bauhinia*, respectively), although present in the same small clade with several other families in Figures 1 and 2, do not form a monophyletic group in any of our searches. Rather than representing a true case of discordance between 18S rDNA and *rbc*L trees, this likely represents either the lower limits of resolution of 18S rDNA sequences (see below) or retrieval of only a small sample of all equally most parsimonious trees (i.e., the strict consensus of all shortest trees, had they been found, would have led to the collapse of this part of the tree). In support of the former conclusion is the observation that more focused phylogenetic studies of 18S sequences representing only Rosidae, some of which swapped to completion, similarly suggest a polyphyletic Fabaceae; bootstrap analyses indicate that these relationships are poorly supported, however (D. Soltis & Soltis, 1997, unpublished).

The position of the monocot genus *Acorus* (Araceae) (Figs. 1, 2) also is unusual. Rather than appearing with the monocots, *Acorus* appears as an early-branching angiosperm, as it did in a previous analysis of 64 18S rDNA and rRNA sequences (Nickrent & Soltis, 1995). Other anomalous placements include the position of Dilleniaceae near the monocots (Figs. 1 and 2) and the unexpected position of *Oncidium* (Orchidaceae) as a first-branching monocot.

Several taxa are noteworthy not only because their phylogenetic positions are unusual, but also because their phylogenetic position varies from search to search. For example, the close relationship of *Gunnera* to the monocots (Figs. 1 and 2) is unexpected, but it is not seen in the trees resulting from analysis of data sets 3 and 4 where *Gunnera* appears in a clade with Santalales, Polygalaceae, and *Pisum* (Fabaceae). The relationship of *Gunnera* also is uncertain in *rbc*L topologies, in which its placement varies from being embedded within Asteridae s.l. (the 476-taxon search) to sister group of the higher dicots (the 499-taxon search).

COMPARISON WITH HAMBY AND ZIMMER (1992)

Hamby and Zimmer (1992) used partial 18S and 26S rRNA sequences to examine relationships among land plants. Because their analyses involved only 46 angiosperms, taxon sampling clearly differs between that and the present study. Nonetheless, brief comparison of the topologies resulting from the two studies is instructive.

In most of the shortest trees obtained here (Figs.

1, 2, 4), as well as in the study of Hamby and Zimmer (1992), *Ceratophyllum* is allied with the monocots. Both studies also concur in suggesting that Nymphaeaceae appear near the base of the angiosperm radiation. Nymphaeaceae are the sister group to all other angiosperms in Hamby and Zimmer's (1992) shortest trees; however, Amborellaceae, Austrobaileyaceae, and Schisandraceae were not included in that study. In all of our shortest trees, Nymphaeaceae follow the latter three families and Illiciaceae as the sister group to all remaining flowering plants.

Another similarity between the shortest trees in both studies is the placement of *Drimys* (Winteraceae). *Drimys* occupies an unusual phylogenetic position in trees presented by both Hamby and Zimmer (1992) and Nickrent and Soltis (1995), appearing as sister to *Glycine* and *Pisum* (Fabaceae), rather than as an early-branching angiosperm. *Drimys* occupies an unusual position in trees derived from the current analyses, as well, appearing among the lower eudicots. In trees resulting from the analysis of data set 3, *Drimys* again appears with *Pisum*. The 18S rDNA sequence of *Drimys* exhibits a number of substitutions not found in other magnoliids. In an attempt to ascertain the relationships of Winteraceae, we sequenced two species of *Drimys*, *D. winteri* and *D. aromatica*, and they have identical sequences. More recently, another member of Winteraceae (*Pseudowintera*) has been sequenced for 18S rDNA (Hoot, unpublished); this sequence is nearly identical to the sequences for *Drimys*. Adding *Pseudowintera* to the analysis does not alter the unusual position of Winteraceae (trees not shown).

The unusual phylogenetic relationships that exist among the eudicots in the shortest trees of Hamby and Zimmer (1992) probably derive from insufficient sampling in that study. The present analysis with its greater representation of eudicots reveals relationships much more in accord with recent classifications (e.g., Cronquist, 1981; Takhtajan, 1987) and/or the *rbc*L topologies of Chase et al. (1993). Thus, the present study suggests that many of the highly unusual relationships seen in Hamby and Zimmer are likely to reflect low taxon density rather than an inherent inability of 18S rDNA sequences to resolve relationships.

CAVEATS

A number of limitations are inherent in any large phylogenetic study such as this. Several factors may contribute to the anomalous positions of certain taxa, including uncertainty regarding maximum parsimony, insufficient taxon sampling and/or density, the presence of "older," erroneous 18S rDNA sequences in the data matrix, and the overall lower rate of evolution of 18S rDNA compared to *rbc*L. We discuss these potential factors in more detail below.

An analysis of this magnitude cannot be expected to achieve maximum parsimony in a reasonable amount of time. It is likely that we did not find all classes of most-parsimonious trees, despite a search strategy (cf. Maddison et al., 1992) designed to identify multiple islands (Maddison, 1991) of shortest trees, and that even shorter trees exist that were not recovered. Furthermore, although our search strategy involved well over two years of computer time, no search swapped to completion; there is no assurance, therefore, that these trees represent even a local parsimony optimum. Although it is, of course, impossible to know how far from completion any search is when it is truncated, the search design used here offers an insightful basis for comparison. Data sets 1 and 2, and 3 and 4 are identical except for the inclusion of two gap characters (indels) in data sets 2 and 4, each of which apparently accounts for only four steps on the shortest trees obtained. Thus, the fact that the shortest trees obtained in searches of data set 2 are seven steps longer than those obtained in searches of data set 1 indicates that the shortest trees obtained in our searches of data set 2 are three steps less parsimonious than trees derived from searches of data set 1. A similar comparison of the searches of data sets 3 and 4 reveals that the shortest trees from searches of data set 4 are two steps less parsimonious than those obtained from data set 3.

We also sampled among the large set of equally parsimonious trees following Sanderson and Doyle (1993b). Using trees obtained in searches of data set 1, we examined the number of distinct components (clades) as a function of the size of the sample of trees (number of trees). We wanted to determine whether increasing the set of trees uncovers new components that bear on the relationships of particular taxa or, in contrast, includes different subsets of the components that are essentially variations on the same theme (Sanderson & Doyle, 1993b). We found that a plot of the number of distinct clades versus the number of trees sampled reaches an asymptote for a small number of trees, suggesting that most of the clade diversity has been found, despite the fact that all most parsimonious trees have not been retrieved. The development of improved methods of phylogenetic analysis of large data sets will ultimately be one of the central issues of phylogeny reconstruction during the next several years (see discussions in Chase et al., 1993; Doyle

et al., 1994; Mishler, 1994; P. Soltis & Soltis, 1997).

Although the anomalous relationships described for some taxa may be unsettling, extremely short branches characterize most of the major clades in the 18S rDNA trees. The internal support for many branches is very low, as indicated by the parsimony jackknife analysis (Farris et al., 1997). Although the monophyly of the angiosperms is well supported (jackknife value of 100%), few major clades within the angiosperms have high jackknife values. For example, large clades such as eudicots and Rosidae do not have jackknife values above 50%; the saxifragoids represent the largest clade having a high jackknife value (jackknife value of 68%). The other monophyletic groups with high jackknife values are relatively small, such as cunonioids, Zingiberales, Malvales, Caryophyllales, Lactoridaceae–Aristolochiaceae, and Schisandraceae–Illiciaceae–Austrobaileyaceae. Significantly, a number of major clades seen in all shortest trees, as well as in trees many steps longer than the most parsimonious trees, do not have jackknife values above 50%, including monocots, glucosinolates, Caryophyllidae s.l., and Asteridae s.l. The majority of high jackknife values correspond to pairs of sister taxa representing terminal nodes (e.g., *Calycanthus–Sassafras, Brexia–Euonymus, Lepuropetalon–Parnassia, Plumbago–Cocoloba, Helwingia–Phyllonoma, Tragopogon–Tagetes, Francoa–Greyia, Trochodendron–Tetracentron, Menispermum–Tinospora*).

Examination of trees obtained from searches that found trees one or a few steps longer than the shortest trees also suggests low internal support for some branches. The phylogenetic position of the monocots appears weakly supported. In some searches of data set 2, for example, trees only one step longer than the shortest trees place the monocots within the eudicots, as part of Rosidae, a position also observed in the shortest trees obtained from searches of data set 3 (Fig. 3). Although all of the starting trees and shortest trees showed Amborellaceae, Illiciaceae, Schisandraceae, and Austrobaileyaceae to be at the base of the angiosperms, one search of data set 2 resulted in trees two steps longer than the shortest trees and placed these four families near the monocots, with *Acorus* and *Oncidium* as the first-branching angiosperms. Trees two steps longer than the shortest trees show the Asteridae s.l. embedded within Rosidae, rather than sister to this large clade. In trees two steps longer than the shortest trees found for data set 3, Caryophyllidae s.l. are not part of Asteridae s.l. but instead are part of the large Rosidae clade.

These few examples illustrate well the uncertainty that surrounds some angiosperm relationships inferred from analyses of 18S rDNA sequences. Furthermore, because relatively few character-state changes occur on many of the branches, a small amount of homoplasy or error in the data set may be sufficient to distort some relationships.

Additionally, some of the anomalous placements could reflect insufficient and/or uneven taxon sampling. The somewhat uneven taxonomic distribution of the sequences presently available means that some groups, such as Asteridae, and much of Rosidae and Hamamelidae, are relatively well represented here, whereas Magnoliidae, the monocots, Dilleniidae, Caryophyllidae, and several orders of Rosidae are under-represented.

The importance of sufficient taxon density is revealed here by some of the differences in topology observed between trees resulting from analyses of the smaller and larger data sets. Many of the taxa not present in the two smaller data sets (3 and 4) represent monosulcates and lower eudicots. It is this portion of the overall topology that shows the most spurious relationships in trees derived from analyses of these two small data sets (the distinction between the monosulcate grade and eudicots largely breaks down in Fig. 3, for example). In contrast, the much more thoroughly represented Asteridae s.l. and Rosidae clades are little affected by slightly decreased representation in data sets 3 and 4. These findings lend further support to the importance of sufficient and equal taxon density in attempts to infer angiosperm phylogeny (e.g., Sytsma & Baum, 1996).

One of the major lessons of this study is that the 18S rRNA gene is difficult to sequence, apparently due in large part to the secondary structure inherent in the rRNA. As a result, many published sequences are erroneous, some highly so, and the extent of insertion and deletion events has been greatly overestimated. We reiterate that whereas the total length of the aligned 18S rDNA data matrix of 64 taxa used by Nickrent and Soltis (1995) was 1853 bp, the length of our 228-taxon data matrix actually is shorter, 1850 bp. After resequencing over 20 dubious 18S rDNA sequences, we were able to remove numerous "false" indels and reduce the length of the aligned sequences. The great majority (70%) of the 18S rDNA sequences used here were generated via cycle sequencing followed by automated sequencing, an approach that provides more reliable rDNA sequences. Additional "older" 18S rDNA sequences should be replaced with sequences generated via this approach.

The overall slower rate of evolution of 18S rDNA compared to *rbc*L (see Nickrent & Soltis, 1995)

contributed, in part, to the widespread belief that 18S rDNA sequences would not contribute greatly to phylogenetic inference in angiosperms. Although this study and other recent papers employing entire 18S rDNA sequences (e.g., Nickrent & Soltis, 1995; Kron, 1996; D. Soltis & Soltis, 1997; Rodman et al., submitted; Johnson et al., unpublished) have dispelled this notion, 18S rDNA sequences will, in most cases, not elucidate relationships to the degree possible with the more rapidly evolving *rbc*L. In some groups such as Orchidaceae, however, 18S rDNA has been found to evolve faster than *rbc*L (Cameron and Chase, unpublished).

FUTURE CONSIDERATIONS

These exploratory analyses clearly illustrate the phylogenetic potential of 18S rDNA sequences for elucidating angiosperm relationships at higher taxonomic levels. Future attempts to conduct broad phylogenetic analyses of 18S rDNA sequences should not only add more taxa, but should also involve the resequencing of the 18S rRNA gene for some of those taxa for which erroneous sequences are suspected.

This study suggests that a broad, nuclear-based phylogenetic hypothesis for the angiosperms is achievable via sequence analysis of the 18S rRNA gene. One of the strengths of 18S sequence data appears to be the ability to recognize a suite of groups that appear in all shortest trees (e.g., glucosinolate clade, saxifragoids, Caryophyllidae s.l., Asteridae s.l., celastroids). This may reflect substitutions that occurred in highly conserved portions of the 18S rRNA gene during the early diversification of a lineage, resulting in a well-supported clade. Such substitutions are rare, however, and the result is limited resolution in some areas of the 18S rDNA topologies. Thus, our results also clearly reveal that 18S rDNA topologies will, in most cases, not exhibit the degree of resolution and internal support possible with *rbc*L sequences. Increased sampling of angiosperms for 18S rDNA sequence analysis is desirable. However, to achieve a nuclear-based estimate of angiosperm phylogeny comparable to that realized with *rbc*L, it probably will be necessary to include all, or portions of, the 26S rRNA gene as well. The utility of portions of the 26S gene for inferring family-level relationships has been demonstrated for angiosperms (Hamby & Zimmer, 1992), as well as for other groups of organisms (e.g., Buchheim & Chapman, 1991; Chapman & Buchheim, 1991; Chapela et al., 1994; Waters et al., 1992).

CONCLUSIONS

This study provides general insights into the structure and evolution of the 18S rRNA gene in angiosperms and dispels certain "myths" about its evolution. Indels are neither as common nor as problematic for alignment as previously believed. Instead, they are largely confined to a few, small, specific regions that correspond to the termini of certain helices present in the proposed secondary structure for 18S rRNA. When these few, short areas are eliminated from consideration, alignment of 18S rDNA sequences is straightforward and easily accomplished by eye across all angiosperms. Conversely, indels are rare throughout most of the 18S rRNA gene; when present, they typically involve a single base pair. Furthermore, indels present in highly conserved regions of the gene may, in fact, be phylogenetically informative, such as the insertion that unites saxifragoids and the deletion that unites higher eudicots.

Initial attempts to evaluate the impact of secondary structure of the 18S rRNA transcript on phylogeny reconstruction in angiosperms suggest that both stem and loop regions appear to be sources of phylogenetic information, with a slightly greater proportion (58% vs. 42%) of informative sites found in stem rather than loop regions. Of the stem changes we analyzed, only 27% destroyed a base-pairing couplet; 73% restored or maintained stem base pairing and hence are considered compensatory. The most frequent type of stem change observed involved single base substitutions that changed one base-pairing couplet to another (e.g., U-G to C-G; U-A to U-G). The high frequency of compensatory change indicates that some down-weighting of stem characters relative to loop bases may be warranted in future broad analyses of 18S rDNA sequences.

The phylogenetic trees obtained in these exploratory, broad analyses of 18S rDNA sequences are largely concordant with those resulting from analyses of *rbc*L sequences. Areas of general concordance include the presence of a tricolpate or eudicot clade, which in turn includes two large clades corresponding mostly to Rosidae and Asteridae s.l., respectively. However, the latter clade also includes Caryophyllidae s.l. in 18S rDNA trees, but not in trees retrieved from analyses of *rbc*L sequences. In addition, the monocotyledons are monophyletic (with the possible exception of *Acorus*) and generally appear with other taxa having monosulcate pollen. One of the most noteworthy differences between this study and that of Chase et al. (1993) concerns the first-branching angiosperms. The

woody magnoliids Amborellaceae, Illiciaceae, Schisandraceae, and Austrobaileyaceae consistently appear as first-branching angiosperms and are always followed by the paleoherb Nymphaeaceae. *Ceratophyllum* is closely allied with the monocots and does not appear as sister to all other angiosperms, as in analyses of *rbc*L sequences (Chase et al., 1993). Monophyletic groups apparent in all analyses include Caryophyllidae s.l., Asteridae s.l., saxifragoids, glucosinolate-producing taxa, santaloids, and cunonioids. Other clades apparent in most analyses include ranunculids and nitrogen-fixing taxa. Thus, this analysis identifies major clades of angiosperms that are largely consistent with those inferred from *rbc*L analyses.

This study further demonstrates that 18S rDNA sequences contain sufficient information to conduct phylogenetic studies at higher taxonomic levels in the angiosperms. Additional phylogenetic analyses of angiosperms should be conducted using a larger 18S rDNA data set that improves taxon sampling for Magnoliidae and Dilleniidae in particular. In constructing this larger data set, some taxa for which published sequences are available should first be resequenced.

Although comparative sequencing of the entire 18S rRNA gene holds great promise for retrieving phylogeny at the family level and above in the angiosperms, this nuclear gene will rarely elucidate familial and generic relationships to the extent possible with *rbc*L (see also Nickrent & Soltis, 1995). Due to the slower rate of evolution of 18S rDNA compared to *rbc*L, it likely will be necessary to sequence the 26S rDNA as well to obtain a nuclear-based estimate of phylogeny comparable to that achieved with *rbc*L. Lastly, because of the general congruence of 18S rDNA and *rbc*L topologies for angiosperms, this study concomitantly suggests that 18S rDNA and *rbc*L sequences should be combined to provide a more accurate estimate of angiosperm phylogeny. One can anticipate that other sequences (e.g., *atp*B and 26S rDNA) will ultimately also be combined with *rbc*L and 18S rDNA sequences to provide a larger data set from which to infer a more complete picture of angiosperm phylogeny.

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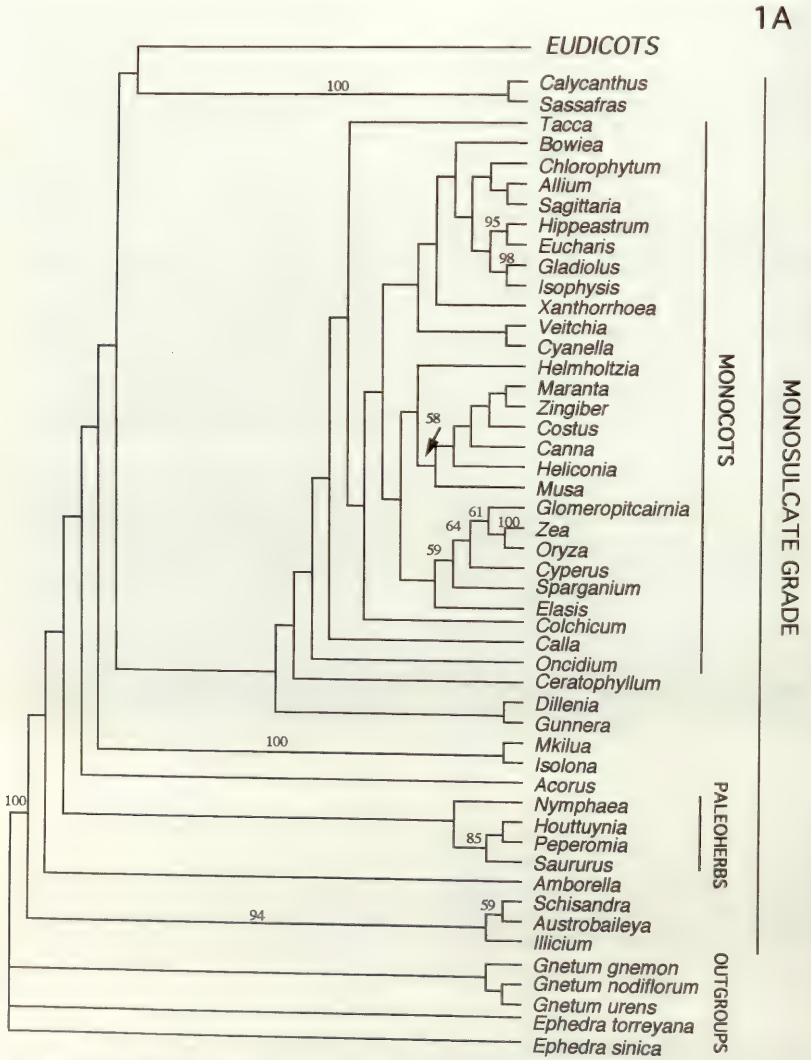


Figure 1. Strict consensus of 5294 shortest trees resulting from the exploratory phylogenetic analysis of 223 species of angiosperms. Each of the shortest trees has a length of 3923 steps, CI = 0.235, and RI = 0.535. Parsimony jackknife values (Farris et al., 1997) of 50 or above (based on 1000 replicates) are given above nodes (run time = 949 sec.). Because of its size, the tree has been broken into four parts (1A, 1B, 1C, and 1D).

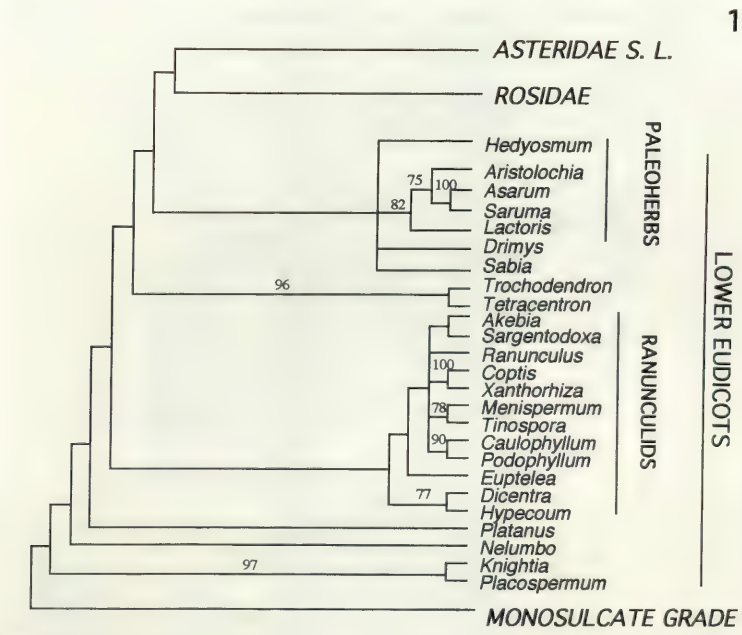

1B
ASTERIDAE S. L.
ROSIDAE
Hedyosmum
Aristolochia
Asarum
Saruma
Lactoris
Drimys
Sabia
Trochodendron
Tetracentron
Akebia
Sargentodoxa
Ranunculus
Coptis
Xanthorhiza
Menispermum
Tinospora
Caulophyllum
Podophyllum
Euptelea
Dicentra
Hypecoum
Platanus
Nelumbo
Knightia
Placospermum
MONOSULCATE GRADE
75
100
82
96
100
78
90
77
97
PALEOHERBS
RANUNCULIDS
LOWER EUDICOTS

Figure 1B.

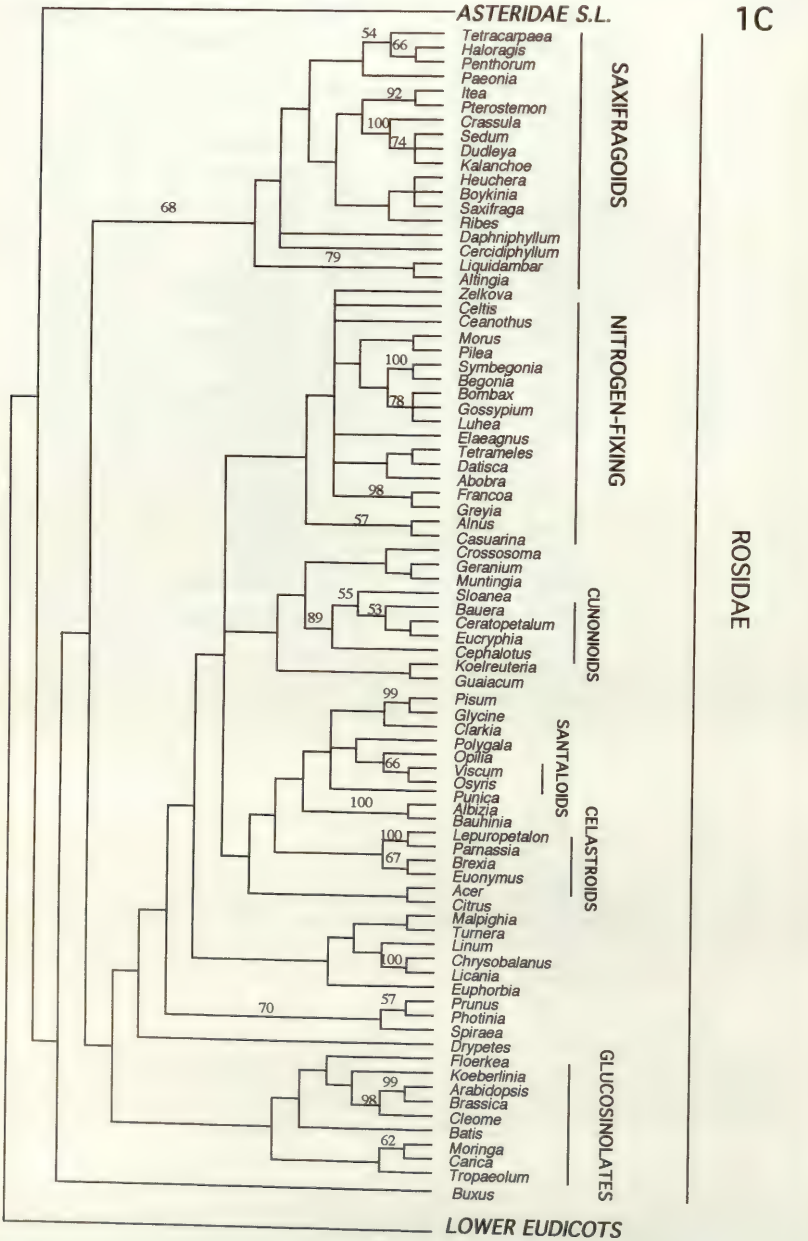

ASTERIDAE S.L.
1C
ROSIDAE
SAXIFRAGOIDS
NITROGEN-FIXING
CUNONIOIDS
SANTALOIDS
CELASTROIDS
GLUCOSINOLATES
Tetracarpaea
Haloragis
Penthorum
Paeonia
Itea
Pterostemon
Crassula
Sedum
Dudleya
Kalanchoe
Heuchera
Boykinia
Saxifraga
Ribes
Daphniphyllum
Cercidiphyllum
Liquidambar
Altingia
Zelkova
Celtis
Ceanothus
Morus
Pilea
Symbegonia
Begonia
Bombax
Gossypium
Luhea
Elaeagnus
Tetrameles
Datisca
Abobra
Francoa
Greyia
Alnus
Casuarina
Crossosoma
Geranium
Muntingia
Sloanea
Bauera
Ceratopetalum
Eucryphia
Cephalotus
Koelreuteria
Guaiacum
Pisum
Glycine
Clarkia
Polygala
Opilia
Viscum
Osyris
Punica
Albizia
Bauhinia
Lepuropetalon
Parnassia
Brexia
Euonymus
Acer
Citrus
Malpighia
Turnera
Linum
Chrysobalanus
Licania
Euphorbia
Prunus
Photinia
Spiraea
Drypetes
Floerkea
Koeberlinia
Arabidopsis
Brassica
Cleome
Batis
Moringa
Carica
Tropaeolum
Buxus
LOWER EUDICOTS

Figure 1C.

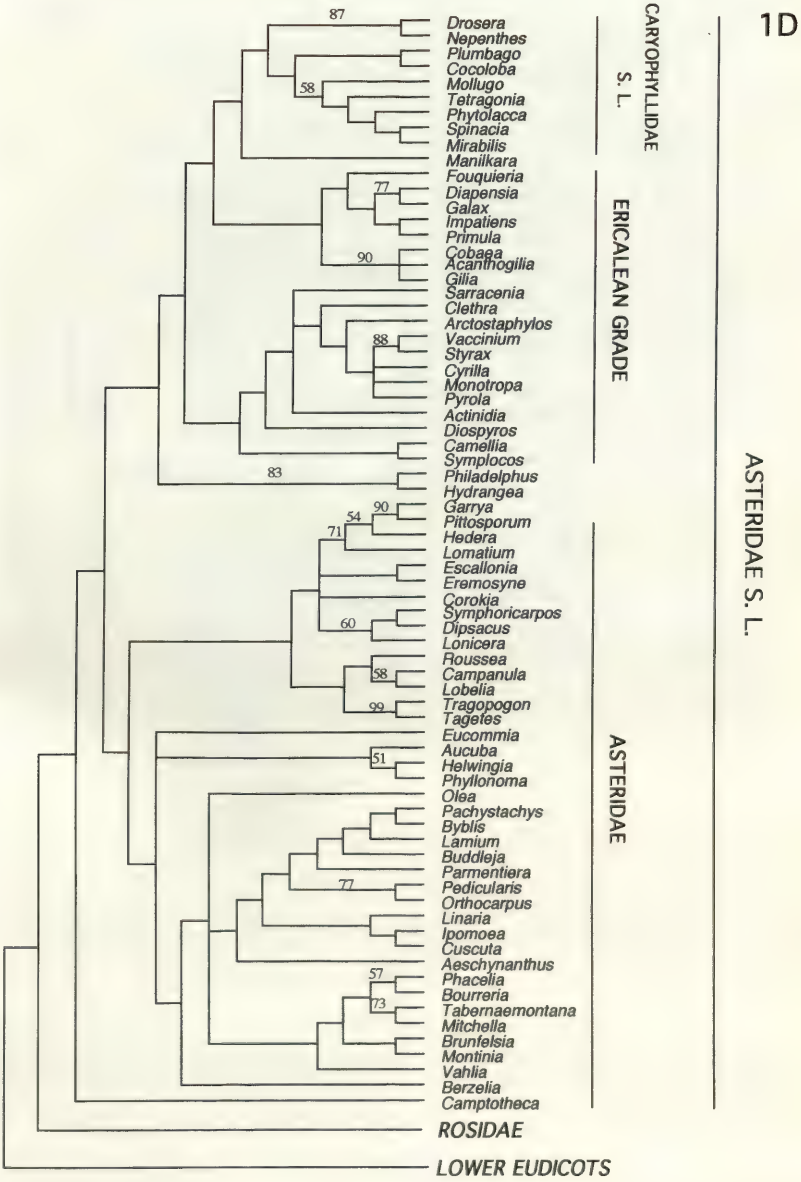

1D
ASTERIDAE S. L.
CARYOPHYLLIDAE S. L.
ERICALEAN GRADE
ASTERIDAE
87
58
77
90
88
83
90
54
71
60
58
99
51
77
57
73
Drosera
Nepenthes
Plumbago
Cocoloba
Mollugo
Tetragonia
Phytolacca
Spinacia
Mirabilis
Manilkara
Fouquieria
Diapensia
Galax
Impatiens
Primula
Cobaea
Acanthogilia
Gilia
Sarracenia
Clethra
Arctostaphylos
Vaccinium
Styrax
Cyrilla
Monotropa
Pyrola
Actinidia
Diospyros
Camellia
Symplocos
Philadelphus
Hydrangea
Garrya
Pittosporum
Hedera
Lomatium
Escallonia
Eremosyne
Corokia
Symphoricarpos
Dipsacus
Lonicera
Roussea
Campanula
Lobelia
Tragopogon
Tagetes
Eucommia
Aucuba
Helwingia
Phyllonoma
Olea
Pachystachys
Byblis
Lamium
Buddleja
Parmentiera
Pedicularis
Orthocarpus
Linaria
Ipomoea
Cuscuta
Aeschynanthus
Phacelia
Bourreria
Tabernaemontana
Mitchella
Brunfelsia
Montinia
Vahlia
Berzelia
Camptotheca
ROSIDAE
LOWER EUDICOTS

Figure 1D.

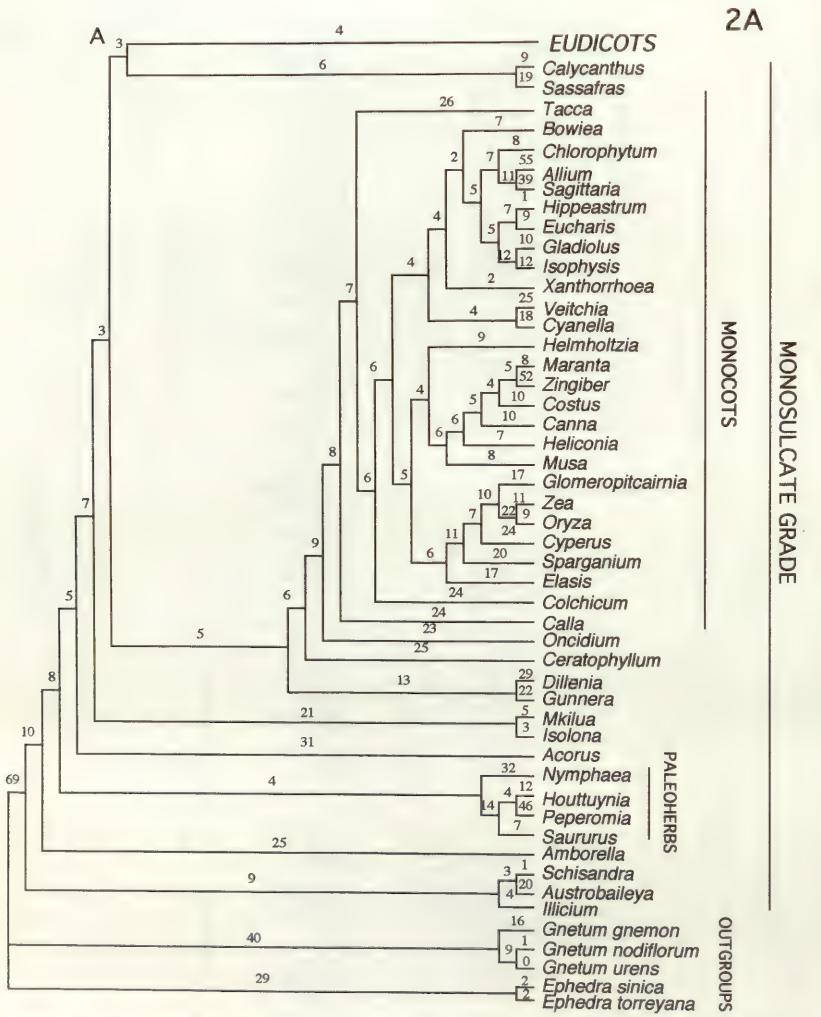


Figure 2. One of 2508 shortest trees resulting from the exploratory phylogenetic analysis of 223 species of angiosperms; two indels were included in the analyses. Each of the shortest trees has a length of 3930 steps, CI = 0.235, and RI = 0.540. Arrows indicate nodes not present in the strict consensus of all shortest trees. The letters A and B indicate the occurrence of the indels described in Table 2. Because of its size, the tree has been broken into four parts (2A, 2B, 2C, and 2D).

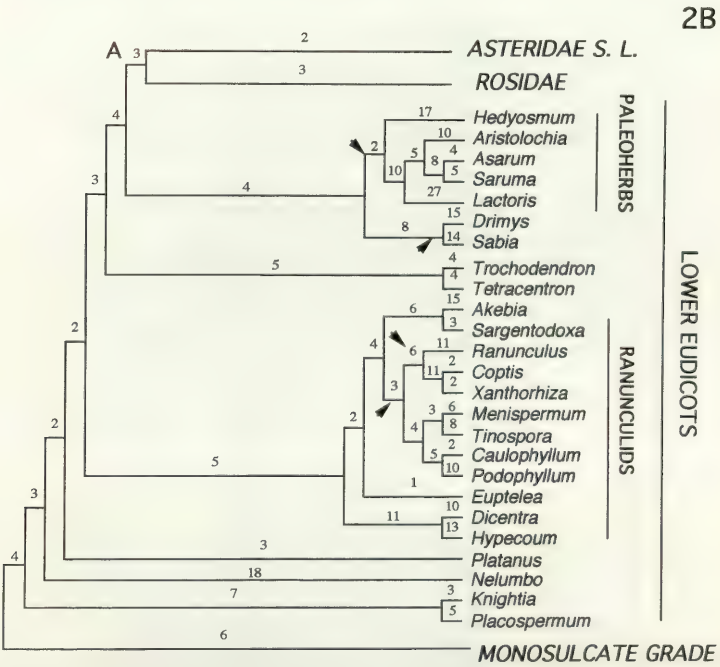

2B
A
ASTERIDAE S. L.
ROSIDAE
Hedyosmum
Aristolochia
Asarum
Saruma
Lactoris
Drimys
Sabia
Trochodendron
Tetracentron
Akebia
Sargentodoxa
Ranunculus
Coptis
Xanthorhiza
Menispermum
Tinospora
Caulophyllum
Podophyllum
Euptelea
Dicentra
Hypecoum
Platanus
Nelumbo
Knightia
Placospermum
MONOSULCATE GRADE
PALEOHERBS
RANUNCULIDS
LOWER EUDICOTS

Figure 2B.

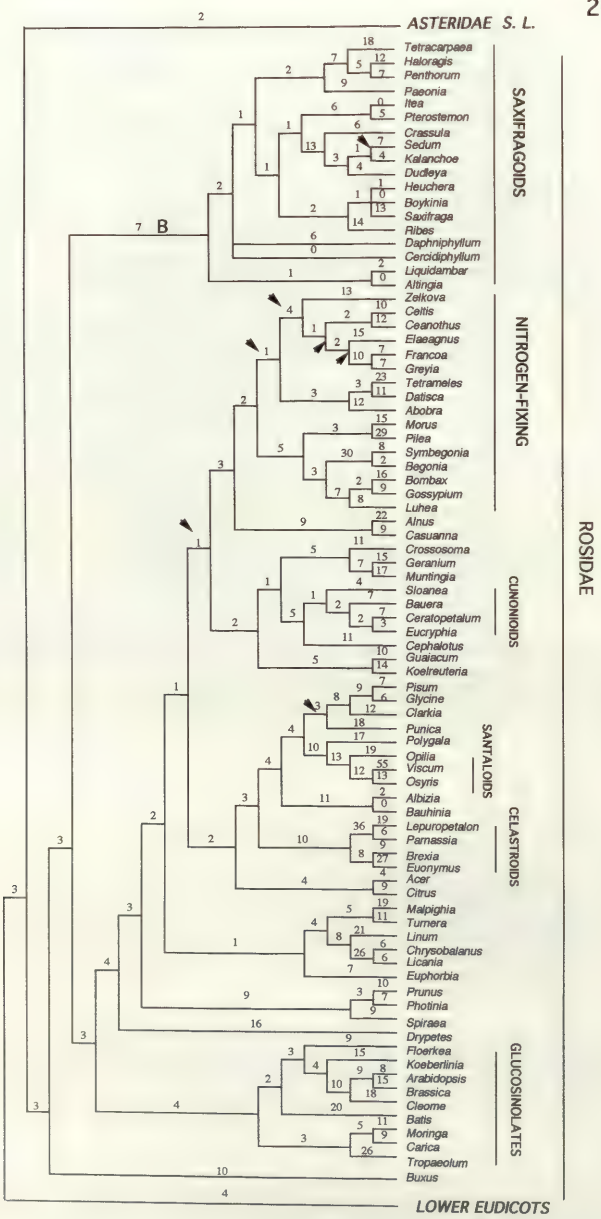

2C
ASTERIDAE S. L.
Tetracarpaea
Haloragis
Penthorum
Paeonia
Itea
Pterostemon
Crassula
Sedum
Kalanchoe
Dudleya
Heuchera
Boykinia
Saxifraga
Ribes
Daphniphyllum
Cercidiphyllum
Liquidambar
Altingia
Zelkova
Celtis
Ceanothus
Elaeagnus
Francoa
Greyia
Tetrameles
Datisca
Abobra
Morus
Pilea
Symbegonia
Begonia
Bombax
Gossypium
Luhea
Alnus
Casuanna
Crossosoma
Geranium
Muntingia
Sloanea
Bauera
Ceratopetalum
Eucryphia
Cephalotus
Guaiacum
Koelreuteria
Pisum
Glycine
Clarkia
Punica
Polygala
Opilia
Viscum
Osyris
Albizia
Bauhinia
Lepuropetalon
Parnassia
Brexia
Euonymus
Acer
Citrus
Malpighia
Turnera
Linum
Chrysobalanus
Licania
Euphorbia
Prunus
Photinia
Spiraea
Drypetes
Floerkea
Koeberlinia
Arabidopsis
Brassica
Cleome
Batis
Moringa
Carica
Tropaeolum
Buxus
LOWER EUDICOTS
B
SAXIFRAGOIDS
NITROGEN-FIXING
CUNONIOIDS
SANTALOIDS
CELASTROIDS
GLUCOSINOLATES
ROSIDAE

Figure 2C.

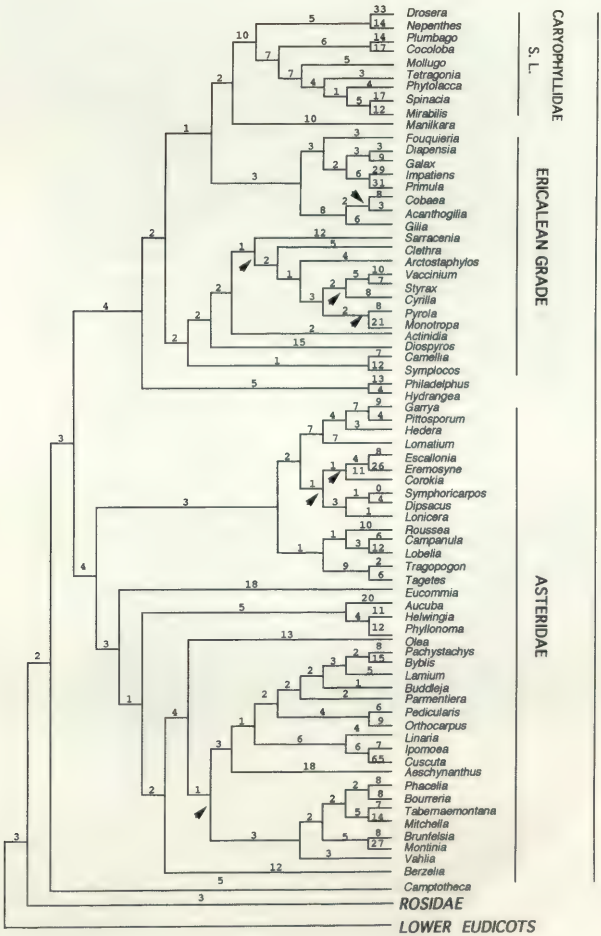

2D
Drosera
Nepenthes
Plumbago
Cocoloba
Mollugo
Tetragonia
Phytolacca
Spinacia
Mirabilis
Manilkara
Fouquieria
Diapensia
Galax
Impatiens
Primula
Cobaea
Acanthogilia
Gilia
Sarracenia
Clethra
Arctostaphylos
Vaccinium
Styrax
Cyrilla
Pyrola
Monotropa
Actinidia
Diospyros
Camellia
Symplocos
Philadelphus
Hydrangea
Garrya
Pittosporum
Hedera
Lomatium
Escallonia
Eremosyne
Corokia
Symphoricarpos
Dipsacus
Lonicera
Roussea
Campanula
Lobelia
Tragopogon
Tagetes
Eucommia
Aucuba
Helwingia
Phyllonoma
Olea
Pachystachys
Byblis
Lamium
Buddleja
Parmentiera
Pedicularis
Orthocarpus
Linaria
Ipomoea
Cuscuta
Aeschynanthus
Phacelia
Bourreria
Tabernaemontana
Mitchella
Brunfelsia
Montinia
Vahlia
Berzelia
Camptotheca
ROSIDAE
LOWER EUDICOTS
CARYOPHYLLIDAE S. L.
ERICALEAN GRADE
ASTERIDAE
ASTERIDAE S. L.

Figure 2D.

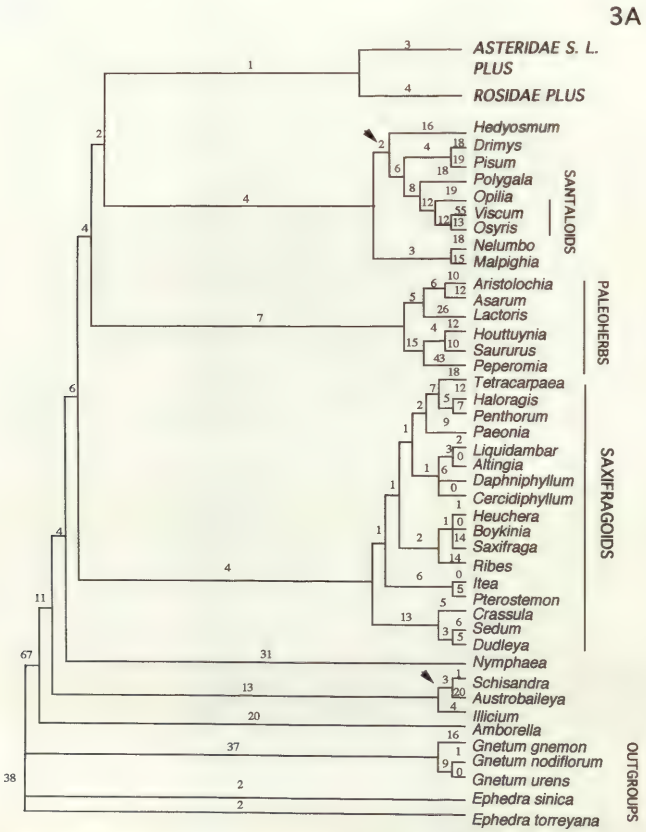


Figure 3. One of 8897 shortest trees resulting from the exploratory phylogenetic analysis of 194 species of angiosperms. Each of the shortest trees has a length of 3501 steps, CI = 0.249, and RI = 0.531. Arrows indicate nodes not present in the strict consensus of all shortest trees. Because of its size, the tree has been broken into three parts (3A, 3B, and 3C).

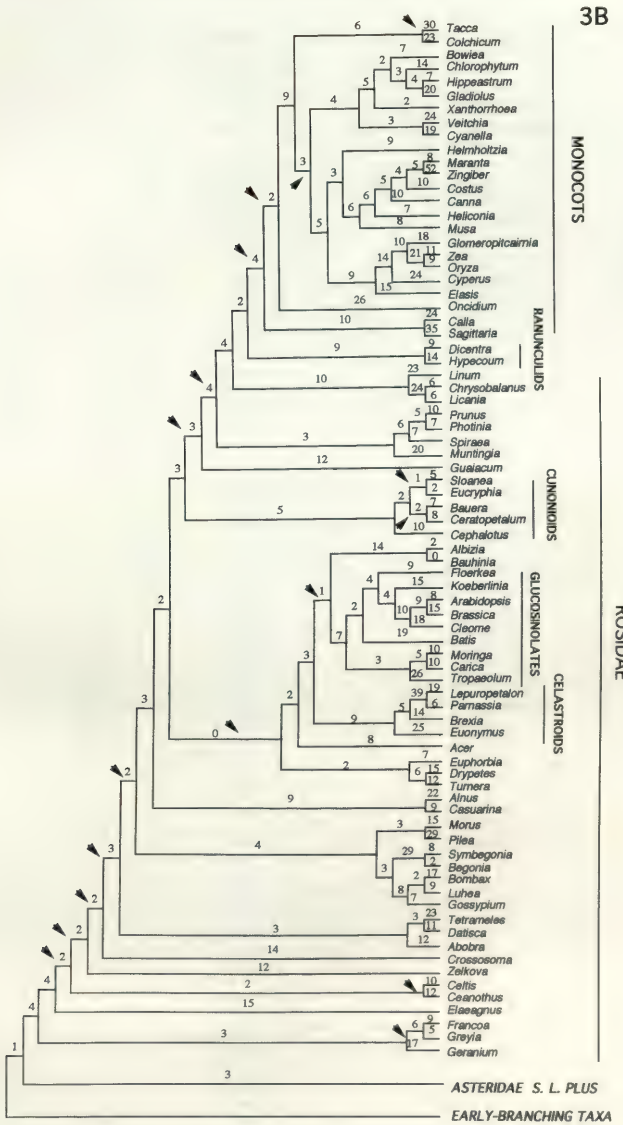

3B
Tacca
Colchicum
Bowiea
Chlorophytum
Hippeastrum
Gladiolus
Xanthorrhoea
Veltchia
Cyanella
Helmholtzia
Maranta
Zingiber
Costus
Canna
Heliconia
Musa
Glomeropitcairnia
Zea
Oryza
Cyperus
Elasis
Oncidium
Calla
Sagittaria
Dicentra
Hypecoum
Linum
Chrysobalanus
Licania
Prunus
Photinia
Spiraea
Muntingia
Guaiacum
Sloanea
Eucryphia
Bauera
Ceratopetalum
Cephalotus
Albizia
Bauhinia
Floerkea
Koeberlinia
Arabidopsis
Brassica
Cleome
Batis
Moringa
Carica
Tropaeolum
Lepuropetalon
Parnassia
Brexia
Euonymus
Acer
Euphorbia
Drypetes
Turnera
Alnus
Casuarina
Morus
Pilea
Symbegonia
Begonia
Bombax
Luhea
Gossypium
Tetrameles
Datisca
Abobra
Crossosoma
Zelkova
Celtis
Ceanothus
Elaeagnus
Francoa
Greyia
Geranium
MONOCOTS
RANUNCULIDS
CUNONIOIDS
GLUCOSINOLATES
CELASTROIDS
ROSIDAE
ASTERIDAE S. L. PLUS
EARLY-BRANCHING TAXA

Figure 3B.

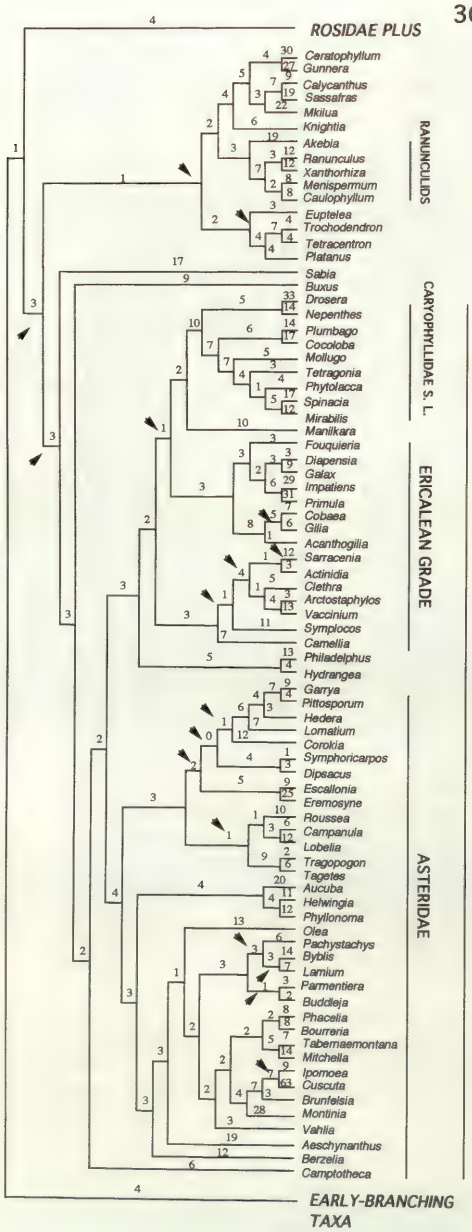

3C
ROSIDAE PLUS
Ceratophyllum
Gunnera
Calycanthus
Sassafras
Mkilua
Knightia
Akebia
Ranunculus
Xanthorhiza
Menispermum
Caulophyllum
Euptelea
Trochodendron
Tetracentron
Platanus
RANUNCULIDS
Sabia
Buxus
Drosera
Nepenthes
Plumbago
Cocoloba
Mollugo
Tetragonia
Phytolacca
Spinacia
Mirabilis
Manilkara
CARYOPHYLLIDAE S. L.
Fouquieria
Diapensia
Galax
Impatiens
Primula
Cobaea
Gilia
Acanthogilia
Sarracenia
Actinidia
Clethra
Arctostaphylos
Vaccinium
Symplocos
Camellia
Philadelphus
Hydrangea
ERICALEAN GRADE
Garrya
Pittosporum
Hedera
Lomatium
Corokia
Symphoricarpos
Dipsacus
Escallonia
Eremosyne
Roussea
Campanula
Lobelia
Tragopogon
Tagetes
Aucuba
Helwingia
Phyllonoma
Olea
Pachystachys
Byblis
Lamium
Parmentiera
Buddleja
Phacelia
Bourreria
Tabernaemontana
Mitchella
Ipomoea
Cuscuta
Brunfelsia
Montinia
Vahlia
Aeschynanthus
Berzelia
Camptotheca
ASTERIDAE
ASTERIDAE S. L.
EARLY-BRANCHING TAXA

Figure 3C.

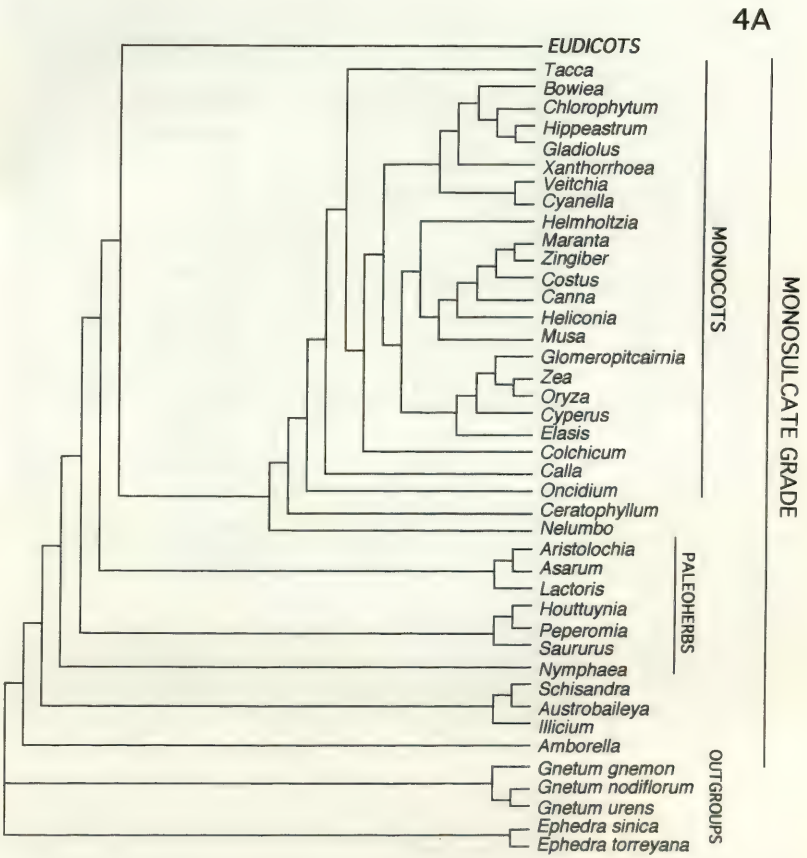


Figure 4. Strict consensus of 2582 shortest trees resulting from the exploratory phylogenetic analysis of 194 species of angiosperms; two indels were included in the analyses. Each of the shortest trees has a length of 3507 steps, CI = 0.249, and RI = 0.536. The letters A and B indicate the occurrence of the indels described in Table 2. Because of its size, the tree has been broken into three parts (4A, 4B, and 4C).

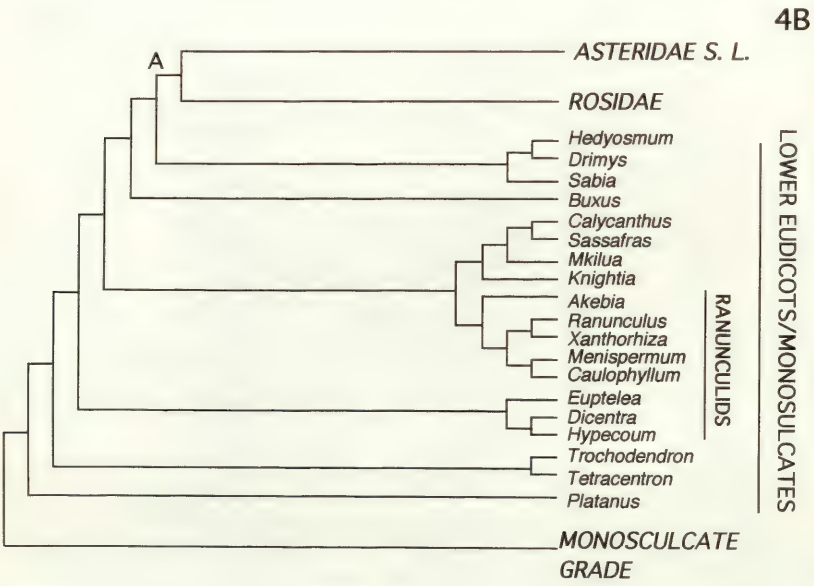

4B
A
ASTERIDAE S. L.
ROSIDAE
Hedyosmum
Drimys
Sabia
Buxus
Calycanthus
Sassafras
Mkilua
Knightia
Akebia
Ranunculus
Xanthorhiza
Menispermum
Caulophyllum
Euptelea
Dicentra
Hypecoum
Trochodendron
Tetracentron
Platanus
MONOSCULCATE
GRADE
RANUNCULIDS
LOWER EUDICOTS/MONOSULCATES

Figure 4B.

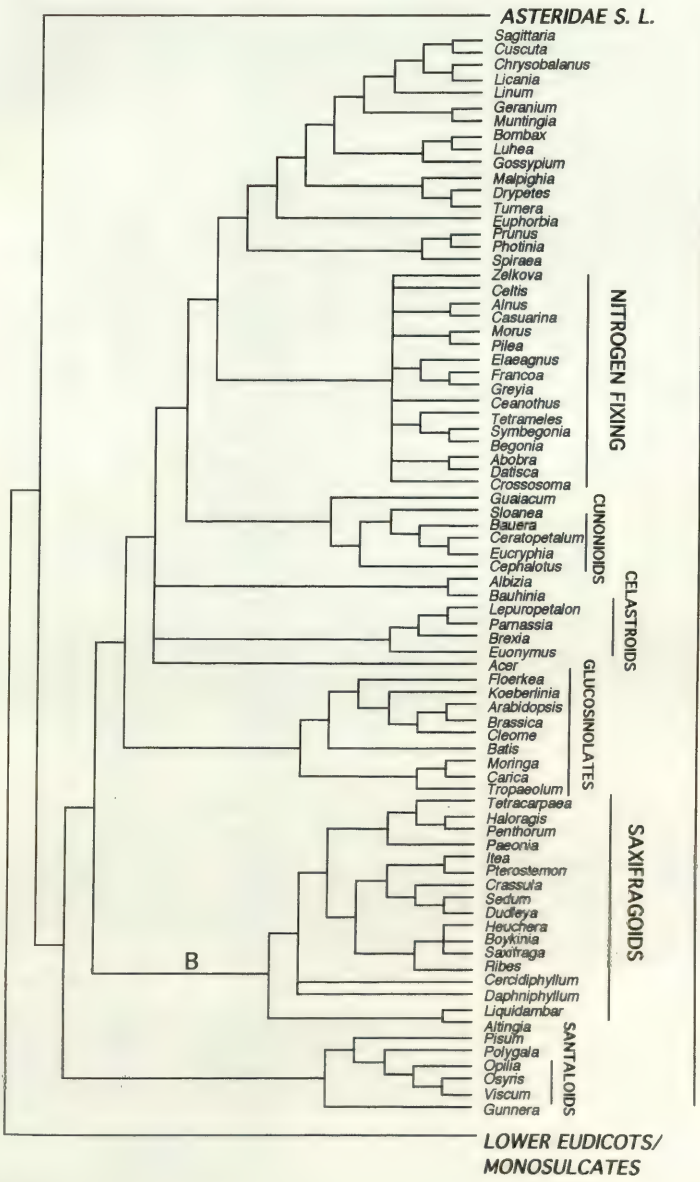

4C
ASTERIDAE S. L.
Sagittaria
Cuscuta
Chrysobalanus
Licania
Linum
Geranium
Muntingia
Bombax
Luhea
Gossypium
Malpighia
Drypetes
Turnera
Euphorbia
Prunus
Photinia
Spiraea
Zelkova
Celtis
Alnus
Casuarina
Morus
Pilea
Elaeagnus
Francoa
Greyia
Ceanothus
Tetrameles
Symbegonia
Begonia
Abobra
Datisca
Crossosoma
Guaiacum
Sloanea
Bauera
Ceratopetalum
Eucryphia
Cephalotus
Albizia
Bauhinia
Lepuropetalon
Parnassia
Brexia
Euonymus
Acer
Floerkea
Koeberlinia
Arabidopsis
Brassica
Cleome
Batis
Moringa
Carica
Tropaeolum
Tetracarpaea
Haloragis
Penthorum
Paeonia
Itea
Pterostemon
Crassula
Sedum
Dudleya
Heuchera
Boykinia
Saxifraga
Ribes
Cercidiphyllum
Daphniphyllum
Liquidambar
Altingia
Pisum
Polygala
Opilia
Osyris
Viscum
Gunnera
NITROGEN FIXING
CUNONIOIDS
CELASTROIDS
GLUCOSINOLATES
SAXIFRAGOIDS
SANTALOIDS
ROSIDAE
B
LOWER EUDICOTS/
MONOSULCATES

Figure 4C.

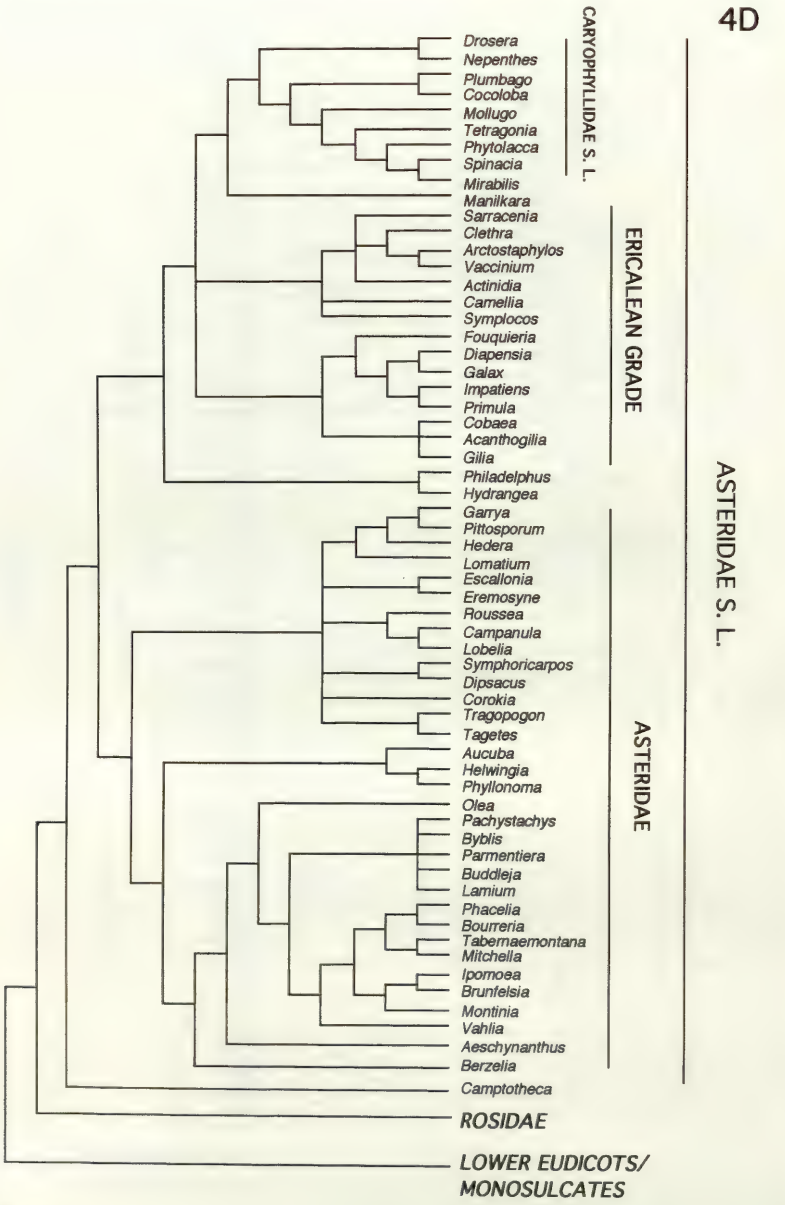
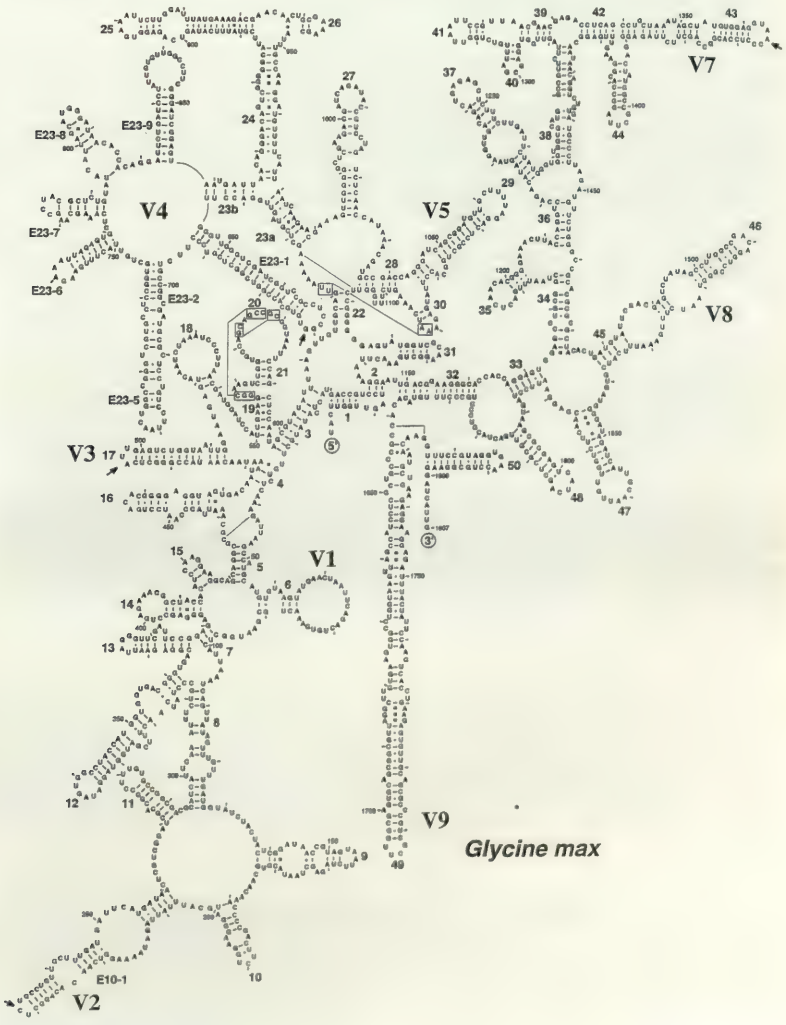

4D
CARYOPHYLLIDAE S. L.
ERICALEAN GRADE
ASTERIDAE
ASTERIDAE S. L.
Drosera
Nepenthes
Plumbago
Cocoloba
Mollugo
Tetragonia
Phytolacca
Spinacia
Mirabilis
Manilkara
Sarracenia
Clethra
Arctostaphylos
Vaccinium
Actinidia
Camellia
Symplocos
Fouquieria
Diapensia
Galax
Impatiens
Primula
Cobaea
Acanthogilia
Gilia
Philadelphus
Hydrangea
Garrya
Pittosporum
Hedera
Lomatium
Escallonia
Eremosyne
Roussea
Campanula
Lobelia
Symphoricarpos
Dipsacus
Corokia
Tragopogon
Tagetes
Aucuba
Helwingia
Phyllonoma
Olea
Pachystachys
Byblis
Parmentiera
Buddleja
Lamium
Phacelia
Bourreria
Tabernaemontana
Mitchella
Ipomoea
Brunfelsia
Montinia
Vahlia
Aeschynanthus
Berzelia
Camptotheca
ROSIDAE
LOWER EUDICOTS/
MONOSULCATES

Figure 4D.

APPENDIX. Proposed secondary structure for the 18S ribosomal RNA of *Glycine max* (modified from Nickrent & Soltis, 1995). This structural model is based on the primary sequence of *Glycine* (Eckenrode et al., 1995) and follows the general models proposed for eukaryotes in general. Tertiary interactions are indicated by thick lines. The positions indicated by arrows are those regions particularly prone to variation in primary sequence and length (positions, 230–237, 496–501; 666–672, 1363–1369); these regions are difficult to align over a broad taxonomic scale and were not included in our phylogenetic analyses (see text).



TRIBAL RELATIONSHIPS IN THE GESNERIACEAE: EVIDENCE FROM DNA SEQUENCES OF THE CHLOROPLAST GENE *ndh*F[1]

J. F. Smith[2], *J. C. Wolfram*[2,3], *K. D. Brown*[2], *C. L. Carroll*[2], *and D. S. Denton*[2]

Abstract

The tribal relationships of the Gesneriaceae are investigated using *ndh*F sequences. A full analysis of 70 taxa including 16 species from the Scrophulariaceae, Bignoniaceae, and Acanthaceae as outgroups, resulted in two most-parsimonious trees of 5610 steps each. In all trees the Gesneriaceae were a monophyletic group and *Paulownia* was the closest single-species outgroup for the analysis. Further analyses eliminated all but the members of the Gesneriaceae and *Paulownia* in order to better assess relationships within the family. The smaller analysis resulted in a single most-parsimonious tree of 4613 steps. The Klugieae are identified as the sister to the remainder of the family and could potentially be separated as a distinct subfamily. The subfamilies Cyrtandroideae (excluding Klugieae) and Gesnerioideae are monophyletic. The placement of Coronanthereae in Cyrtandroideae does not have support from this analysis, whereas its placement in Gesnerioideae is supported. Alternatively, Coronanthereae could be segregated as a separate subfamily but in order to avoid a paraphyletic Gesnerioideae would either include the Napeantheae and Beslerieae or elevate these two tribes to an additional subfamily. Within Gesnerioideae the genus *Sinningia* is removed from the tribe Gloxinieae into the Sinningieae, which also contains the recently combined species *Sinningia brasiliensis* (*Lietzia*), as well as *Paliavana* and *Vanhouttea*. The Episcieae, Gesnerieae, Napeantheae, and Beslerieae are identified as monophyletic groups, as are the remainder of the Gloxinieae with *Sinningia* sensu lato removed. Within Cyrtandroideae, several well-supported, monophyletic lineages within the large, heterogeneous tribe Didymocarpeae are identified, and with the current data the tribe Trichosporeae appears to be polyphyletic. The distribution of chromosome numbers, nodal anatomy, placental structure, and stem modification are examined based on these molecular trees.

Investigations of higher level cladistic relationships (generic, familial, and above) have recently drawn a great deal of attention (*Annals of the Missouri Botanical Garden* Vol. 80(3); Olmstead et al., 1992, 1993; Donoghue et al., 1992; Cantino, 1992; Judd et al., 1994). These analyses have provided tremendous insights toward our classification system and process of classification, frequently drawing attention to families that have been separated on the basis of primarily woody versus herbaceous taxa (Cantino, 1992; Judd et al., 1994) or tropical versus temperate (Judd et al., 1994). More recently an investigation of the Lamiales sensu lato has indicated that the largest family in this order, Scrophulariaceae, is unlikely to be a monophyletic group (Olmstead et al., 1992, 1993; Olmstead & Reeves, 1995). A thorough investigation of the Scrophulariaceae utilizing DNA sequences from both the *rbc*L and *ndh*F genes has indicated that the family is comprised of at least two monophyletic groups with several genera not having any strict affinity to the Scrophulariaceae or other related families included in the analysis (Olmstead & Reeves, 1995). Likewise, Olmstead and Reeves (1995) found that several families traditionally segregated from the Scrophulariaceae are best included as members of one of the two major lineages (e.g., Plantaginaceae).

Although most members of the Lamiales s.l. are temperate, there are some primarily tropical groups (Gesneriaceae, Acanthaceae, Bignoniaceae). In order to better assess whether the division between these families represents another artificial segregation based on distribution (tropical vs. temperate) or woody versus herbaceous (e.g., Bignoniaceae vs. Gesneriaceae), a thorough investigation of the Gesneriaceae was deemed necessary to complement the investigations that have already demonstrated monophyly of Acanthaceae (Scotland et al., 1995) and Bignoniaceae (R. Olmstead, pers. comm.), but have not sampled widely in the Gesneriaceae.

[1] We are indebted to the following for sharing plant material: L. E. Skog, W. L. Wagner, J. K. Boggan, Strybing Arboretum, M. Källersjö, B. Nordenstam, R. Dunn, D. Turley, J. Katzenstein, B. Stewart, M. Evans, and the American Gesneriad and Gloxinia Society (AGGS) seed fund. We also thank Richard Olmstead and Michael Kiehn for helpful comments on the manuscript. Funding for this project was provided by NSF grant DEB-9317775 and a grant from AGGS to JFS.

[2] Department of Biology, Boise State University, 1910 University Drive, Boise, Idaho, 83725, U.S.A.

[3] Current address: 1263 Londonderry, Idaho Falls, Idaho, 83404, U.S.A.

The Gesneriaceae are a mid-sized to large plant family comprising approximately 2500–3500 species in 120–135 genera, distributed primarily in the tropics with a few temperate species in Europe, China, and Japan (Heywood, 1978; A. Weber, pers. comm.). The majority of species in the Gesneriaceae are herbaceous perennials, but can be annuals, shrubs, lianas, and trees. Many species (20%) are epiphytic, and the Gesneriaceae rank among the top ten plant families in terms of absolute numbers of epiphytic taxa (Madison, 1977; Kress, 1986). Given the diverse habits of the Gesneriaceae, it is not surprising that there is a wide array of morphological variation within the family. Corolla tubes may be long and prominent as in *Columnea* L., or short as in *Saintpaulia* Wendl. Leaves are opposite in the majority of the family, but anisophylly, leading to an alternate arrangement with abscission of the smaller leaf, is common. Many of these morphologically diverse features of the Gesneriaceae are hypothesized as adaptations to the epiphytic habit (Ackerman, 1986).

The Gesneriaceae are a member of the Lamiales s.l. and are distinguished from other families in the order by the combination of five-lobed corollas, parietal placentation, and presence of endosperm in most taxa (Cronquist, 1981). However, because many of these characters vary within some members of the Gesneriaceae (including variation within individuals of some species), there has been considerable confusion regarding the placement of some genera. For example, members with axile placentation can be classified incorrectly with the Scrophulariaceae, and those genera lacking endosperm potentially may be classified with the Acanthaceae and Bignoniaceae.

There have been relatively few cladistic analyses performed within the Gesneriaceae (Kvist, 1990; Crisci et al., 1991; Boggan, 1991; Smith & Sytsma, 1994a, b, c; Smith, 1996), and only one (Smith, 1996) performed at the tribal level. A cladistic analysis is desirable to help resolve relationships, to determine if the family is monophyletic, and to improve classification within the family by rearranging tribes and subfamilies to reflect phylogenetic relationships.

Classifications of the Gesneriaceae traditionally recognize two subfamilies (Gesnerioideae and Cyrtandroideae) (Bentham, 1876; Burtt, 1962, 1977; Fritsch, 1893, 1894), but others have included an additional subfamily (Coronantheroideae: Wiehler, 1983; Episcioideae: Ivanina, 1965). The division of the family is largely based on the uniform (Gesnerioideae), or uneven (Cyrtandroideae) enlargement of the cotyledons after germination (Burtt, 1962). Another character that has been useful in separating the subfamilies is the presence (Gesnerioideae) or absence (Cyrtandroideae) of endosperm in the seed. In addition, the Gesnerioideae have a neotropical distribution and most species have inferior or semi-inferior ovaries, whereas the Cyrtandroideae are primarily paleotropical with superior ovaries. However, the geographic distribution and ovary position are not consistent within the subfamilies. Therefore, although the Cyrtandroideae can be defined by a synapomorphic character (uneven cotyledon development), the Gesnerioideae have been characterized by a symplesiomorphic character common to dicotyledons in general.

The two subfamilies have been divided further into 9–17 tribes (Bentham, 1876; Burtt, 1962, 1977; Fritsch, 1893, 1894; Ivanina, 1965; Wiehler, 1983; Burtt & Wiehler, 1995). The classification schemes differ due to the characters emphasized. For example, Fritsch (1893, 1894) placed the Columneae in the Cyrtandroideae based on their superior ovary. Later, the Columneae were moved to the Gesnerioideae due to the presence of uniform cotyledons (Burtt, 1962, 1977) and combined into the Episcieae based on nodal anatomy (Wiehler, 1983). This paper presents a cladistic analysis of DNA sequences in order that phylogenetic relationships among taxa may be more clearly resolved, and a more stable classification scheme proposed.

The gene *ndh*F is a chloroplast gene that in tobacco encodes a protein of 740 amino acids presumed to be a subunit of an NADH dehydrogenase (Sugiura, 1992). The use of *ndh*F sequences for systematic studies has provided a far greater number of characters to resolve relationships than studies using *rbc*L. The reasons for the increased number of characters are that the gene is approximately 50% longer than *rbc*L (2103 vs. 1431 bp in tobacco [Wolfe, 1991]) and has a nucleotide substitution rate that is approximately two times higher than *rbc*L based on comparisons of rice and tobacco (Sugiura, 1989). In recent studies using this gene in the Acanthaceae, Scotland et al. (1995) found three times the number of characters compared to *rbc*L, and Olmstead and Sweere (1994) discovered 60% more variable characters with *ndh*F in the Solanaceae. Likewise, Clark et al. (1995) have found that *ndh*F sequences are informative for resolving relationships within the Poaceae, and Olmstead and Reeves (1995) have resolved several clades in a polyphyletic Scrophulariaceae. The larger number of variable characters makes *ndh*F sequences ideal for taxonomic groups that have not been resolved well using *rbc*L data, such as members of the As-

Table 1. Species sequenced in this study with Genbank submission numbers and voucher specimens. JFS - James F. Smith, WLW - Warren L. Wagner, DEB - Dennis E. Breedlove, SI - Smithsonian Institution, LG - Longwood Gardens. Letters in parentheses indicate herbarium where vouchers are deposited.

Species	Voucher	Genbank number
Achimenes skinneri Lindl.	SI 94-606	U62177
Aeschynanthus micranthus C. B. Clarke	JFS 643 (WIS)	U62169
Agalmyla parasitica (Lam.) Kuntze	SI 94-570	U62171
Alloplectus meridensis Klotzsch	JFS 1182 (WIS)	U62158
Anna mollifolia (W. T. Wang) W. T. Wang & K. Y. Pan	Skog 94-498	U62188
Asteranthera ovata (Cav.) Hanst.	Stewart 12234 (SRP)	U62204
Besleria affinis Morton	LG870575	U62162
Boea hygroscopica F. Muell.	SI 89-041	U62205
Chirita sinensis Lindl.	SI 94-111	U62189
Codonanthe elegans Wiehler	SI 82-45	U62178
Columnea schiedeana Schlecht.	JFS 288 (WIS)	U62164
Cyrtandra hawaiensis C. B. Clarke	WLW 6753 (BISH)	U62172
Cyrtandra umbellifera Merr.	WLW 6701 (BISH)	U62165
Cyrtandromoea acuminata Benth. & Hook.	JFS 3539 (SRP)	U62173
Diastema racemiferum Benth.	SI 85-98	U62156
Didissandra frutescens Clarke	SI 94-512	U62190
Didymocarpus albomarginata Hemsl.	SI 94-509	U62207
Drymonia stenophylla (J. D. Smith) H. E. Moore	JFS 2248 (WIS)	U62159
Fieldia australis Cunn.	Stewart s.n. (SRP)	U62196
Gasteranthus corallinus (Fritsch) Wiehler	SI 94-243	U62163
Gesneria pedicellaris Alain	SI 94-567	U62192
Gesneria christii Urban	SI 94-507	U62191
Gloxinia sylvatica (HBK) Kunth	Dunn 9012051 (SRP)	U62157
Hemiboea henryi C. B. Clarke	SI 85-157	U62180
Kohleria spicata (Kunth) Oerst.	SI 94-552	U62181
Lysionotus pauciflorus Maxim.	SI 94-158	U62182
Mitraria coccinea Cav.	Stewart s.n. (SRP)	U62193
Monophyllaea hirticalyx Franch.	no voucher	U62168
Monopyle macrocarpa Benth.	no voucher	U62197
Napeanthus costaricensis Wiehler	no voucher	U62198
Napeanthus macrostoma Leeuwenberg	Feuillet (US)	U62161
Negria rhabdothamnoides F. Muell.	Nordenstam 8608 (S)	U62195
Nematanthus hirsutus (Mart.) Wiehler	Olmstead & Reeves, 1995	L36404
Niphaea oblonga Lindl.	SI 78-354	U62160
Opithandra primuloides (Miq.) B. L. Burtt	SI 93-073	U62183
Ornithoboea wildeana Craib.	SI 93-075	U62166
Paliavana prasinata (Ker-Gawl.) Fritsch	SI 78-368	U62174
Paraboea rufescens (Franch.) Burtt	Skog s.n. (US)	U62206
Petrocosmea flaccida Craib	SI 85-196	U62184
Primulina tabacum Hance	SI 93-040	U62167
Ramonda myconi (L.) Rchb.	Katzenstein s.n. (SRP)	U62185
Rhynchoglossum notonianum (Wall.) B. L. Burtt	SI 94-378	U62179
Rytidophyllum tomentosum (L.) Mart.	SI 77-235	U62200
Rytidophyllum auriculatum Hook.	SI 94-524	U62199
Saintpaulia rupicola B. L. Burtt	SI 94-492	U62176
Sarmienta repens Ruiz & Pavón	Stewart s.n. (SRP)	U62194
Sinningia (Lietzia) brasiliensis (Regel & Schmidt) Wiehler	Dunn 9104014 (SRP)	U62175
Sinningia cooperi (Paxt.) Wiehler	SI 94-340	U62201
Sinningia richii Clayb.	SI 94-554	U62186
Solenophora obliqua D. L. Denham & D. N. Gibson	DEB 71542 (CAS)	U62202
Streptocarpus holstii Engl.	Olmstead & Reeves, 1995	L36415
Streptocarpus saxorum Engl.	JFS s.n. (WIS)	U62170
Titanotrichum oldhamii (Hemsl.) Soler.	SI 86-106	U62187

Table 1. Continued.

Species	Voucher	Genbank number
Vanhouttea lanata Fritsch	SI 94-516	U62203
Outgroups		
Antirrhinum majus L.	Olmstead & Reeves, 1995	L36392
Brillantaisia lamium Benth.	Scotland et al., 1995	U12654
Catalpa sp.	Olmstead & Reeves, 1995	L36397
Celsia arcturus Jacq.	Olmstead & Reeves, 1995	L36398
Crabbea reticulata C. B. Clarke	Scotland et al., 1995	U12655
Crossandra nilotica Oliv.	Scotland et al., 1995	U12656
Digitalis grandiflora Mill.	Olmstead & Reeves, 1995	L36399
Hygrophila corymbosa Lindau	Scotland et al., 1995	U12661
Martinella obovata (HBK) Bureau & K. Schum.	Olmstead & Reeves, 1995	L36402
Paulownia tomentosa Steud.	Olmstead & Reeves, 1995	L36406
Selago thunbergii Choisy	Olmstead & Reeves, 1995	L36412
Schlegelia parviflora (Oerst.) Monachino	Olmstead & Reeves, 1995	L36410
Scrophularia sp.	Olmstead & Reeves, 1995	L36411
Tabebuia heterophylla (A. de Candolle) Britton	Olmstead & Reeves, 1995	L36416
Verbascum thapsus L.	Olmstead & Reeves, 1995	L36417
Veronica catenata Pennell	Olmstead & Reeves, 1995	L36419

teridae and Lamiales s.l. (Olmstead et al., 1992, 1993; Chase et al., 1993).

Materials And Methods

The gene sequences used in this analysis were generated by thermal cycle sequencing (Innis et al., 1988) of previously amplified *ndh*F regions. The *ndh*F gene was amplified in two overlapping sections (positions 1–1350, and 972–2044) from genomic DNA isolated from fresh, frozen, or silica gel dried material (Smith et al., 1992). Once amplification products were obtained, the sample was purified using PCR wizard purification preps (Promega) according to the manufacturer's instructions. The purified DNA then was subjected to cycle sequencing using the Silver Sequence method (Promega). This sequencing method resulted in sequences that could be read within six to eight hours after amplification was completed. The products of one round of amplification provided sufficient material for completing the gene sequences described here. The advantages of the silver staining procedure over radioactive methods are safety, minimal waste disposal, and speed.

Choice of Taxa

The focus of this analysis was on the tribal relationships of the Gesneriaceae and comparison of the results of this analysis with one based on morphological data (Smith, 1996). Genera were selected to represent current and previous tribal classifications within the family and, whenever possible, to match genera used in the morphological analysis. In some instances, a genus that had been used with the morphological analysis (Smith, 1996) was not readily available for the molecular analysis. Therefore this molecular analysis contains many taxa that have not been included in the morphological analysis, and direct comparisons will be made with a reduced data set at a future date. The species used in the analysis, voucher information, and Genbank accession numbers are included in Table 1.

Genera have been selected to represent the most recent tribal classifications with two to ten genera from each tribe (Tables 2 and 3). In order to represent current classification systems along with earlier systems, 48 genera were selected (Tables 2 and 3).

Outgroup Selection

Outgroups were selected to root the tree representing tribal relationships within Gesneriaceae. The best method for doing this is by outgroup comparison (Donoghue & Cantino, 1984; Maddison et al., 1984). The most appropriate outgroup for the tribes of the Gesneriaceae should be the most closely related plant family or clade. The Gesneriaceae have been placed in the order Lamiales s.l. in the subclass Asteridae (or equivalent groups of families) in numerous taxonomic treatments (Dahlgren, 1975; Thorne, 1976, 1983, 1992; Heywood, 1978; Takhtajan, 1980; Cronquist, 1981). However,

Table 2. Genera of Gesnerioideae (Burtt & Wiehler, 1995) used and their classification status. NT = not treated. Subfamilial names are underlined to readily distinguish them from tribal names. Subtribal names are abbreviated as Colum. - Columneineae, Codon. - Codonanthinae.

Genus	Wiehler, 1983	Ivanina, 1965	Fritsch, 1893–94
	Gesnerioideae	Gesnerioideae	Gesnerioideae
Achimenes	Gloxinieae	Gloxinieae	Gloxinieae
Gloxinia	Gloxinieae	Gloxinieae	Gloxinieae
Monopyle	Gloxinieae	Bellonieae	Bellonieae
Niphaea	Gloxinieae	Bellonieae	Bellonieae
Kohleria	Gloxinieae	Kohlerieae	Kohlerieae
Diastema	Gloxinieae	Kohlerieae	Kohlerieae
Sinningia	Gloxinieae	Kohlerieae	Sinningieae
Vanhouttea	Gloxinieae	Kohlerieae	Kohlerieae
Paliavana	Gloxinieae	Reichsteinerieae	Kohlerieae
Lietzia	Gloxinieae	Reichsteinerieae	Sinningieae
Solenophora	Gloxinieae	Solenophoreae	Solenophoreae
Gesneria	Gloxinieae	Gesnerieae	Gesnerieae
Rytidophyllum	=Gesneria	Gesnerieae	Gesnerieae
		Episcioideae	Cyrtandroideae
Columnea	Episcieae	Columneae	Columneae-Colum.
Codonanthe	Episcieae	Columneae	Columneae-Codon.
Nematanthus	Episcieae	Columneae	Columneae-Colum.
Alloplectus	Episcieae	Episcieae	Columneae-Colum.
Drymonia	Episcieae	Episcieae	Columneae-Colum.
Besleria	Beslerieae	Episcieae	Beslerieae
Gasteranthus	Beslerieae	NT	NT
Napeanthus	Napeantheae	Episcieae	Klugieae
	Coronantheroideae	Cyrtandroideae	
Asteranthera	Coronanthereae	Mitrarieae	Coronanthereae
Sarmienta	Coronanthereae	Mitrarieae	Coronanthereae
Mitraria	Coronanthereae	Mitrarieae	Coronanthereae
Fieldia	Coronanthereae	Mitrarieae	Coronanthereae
Negria	Coronanthereae	Coronanthereae	Coronanthereae

the relationships among these families are somewhat ambiguous. A recent cladistic analysis of these families based on DNA sequencing of the chloroplast encoded *rbc*L gene resulted in poor resolution of the relationships of these families (Olmstead et al., 1993), although these relationships have been more resolved with the addition of *ndh*F sequences (Olmstead & Reeves, 1995).

Three families from the Lamiales s.l. were used as outgroups for this analysis. These were the Acanthaceae, Bignoniaceae, and Scrophulariaceae. Sequences for sixteen species of these three families were obtained via Genbank (Table 1; Olmstead & Reeves, 1995; Scotland et al., 1995) and included representatives from three lineages identified within the Scrophulariaceae (Olmstead & Reeves, 1995). Initial analyses used all 16 species as the outgroup. Subsequent analyses used only Gesneriaceae with *Paulownia* Sieb. & Zucc. as the outgroup.

PHYLOGENETIC ANALYSIS

Phylogenetic divergence was reconstructed using PAUP version 3.1.1 (Swofford, 1993) to implement Wagner parsimony (Farris, 1970; Farris et al., 1970; Swofford & Maddison, 1987). This program allows parallelisms and reversals (homoplasy), and provides an option for missing data. In this analysis, trees were generated using the general heuristic option, saving minimal trees only, with the collapse zero-length branches, and ignore uninformative characters options in effect. Because of the large number of taxa in this analysis, the branch and bound and exhaustive search options would have consumed an excessive amount of time. Therefore, the trees presented here are best approximations and not exact solutions. The manner in which the program reconstructs phylogenetic sequences is sensitive to the order of taxa presentation in the data matrix, frequently finding islands of equally parsimonious trees depending on the order (Mad-

Table 3. Genera of Cyrtandroideae (Burtt & Wiehler, 1995) used and their classification status. NT = not treated. The tribe, Didymocarpeae, is abbreviated Didy. in order to show the subtribal classification system of Ivanina (1965) and Fritsch (1893, 1894).

Genus	Burtt, 1962,77	Ivanina, 1965	Fritsch, 1893–94
Ramonda	Didymocarpeae	Ramondeae	Ramondeae
Saintpaulia	Didymocarpeae	Saintpaulieae	Ramondeae
Opithandra	Didymocarpeae	Didy.-Roettlerineae	NT
Didymocarpus	Didymocarpeae	Didy.-Roettlerineae	Didy.-Roettlerineae
Didissandra	Didymocarpeae	Didy.-Roettlerineae	Didy.-Oreacharineae
Anna	Didymocarpeae	Didy.-Roettlerineae	NT
Chirita	Didymocarpeae	Didy.-Roettlerineae	Didy.-Roettlerineae
Petrocosmea	Didymocarpeae	Didy.-Roettlerineae	Ramondeae
Titanotrichum	anomalous	NT	NT
Cyrtandromoea	Loxonieae/Scroph.	Klugieae	Beslerieae
Paraboea	Didymocarpeae	Didy.-Roettlerineae	Didy.-Roettlerineae
Boea	Didymocarpeae	NT	Streptocarpeae
Hemiboea	Didymocarpeae	Didy.-Roettlerineae	NT
Primulina	Didymocarpeae	Didy.-Roettlerineae	Klugieae
Streptocarpus	Didymocarpeae	Didy.-Streptocarp.	Streptocarpeae
Ornithoboea	Didymocarpeae	Didy.-Streptocarp.	Streptocarpeae
Aeschynanthus	Trichosporeae	Trichosporeae	Trichosporeae
Agalmyla	Trichosporeae	Trichosporeae	Trichosporeae
Lysionotus	Trichosporeae	Trichosporeae	Trichosporeae
Cyrtandra	Cyrtandreae	Cyrtandreae	Cyrtandreae
Rhynchoglossum	Klugieae	Klugieae	Klugieae
Monophyllaea	Klugieae	Klugieae	Beslerieae

dison, 1991). Therefore, it is important to repeat the analysis several times. To do this, the search strategy of Olmstead and Palmer (1994) was implemented: searching for 1000 trees each in five subsequent analyses with the nearest neighbor interchange (NNI) search option in effect and mulpars "off." Each of the results from the five NNI searches was used as the starting tree(s) for a search with tree bisection reconnection (TBR) and mulpars "on." This strategy was used in the full analysis with all 16 non-Gesneriaceae taxa designated as outgroups. Likewise, the same strategy was used with only the members of the Gesneriaceae and *Paulownia* as the outgroup, and with constraints options.

Branch support analysis was performed to examine trees that were six or fewer steps longer than the most-parsimonious tree (Bremer, 1988; Donoghue et al., 1992; Bremer, 1994). This type of analysis provides an indication of the robustness of the data by determining which clades persist in a consensus tree as parsimony is relaxed. This analysis was performed by saving all trees six steps longer than the most-parsimonious trees and then examining subsets of trees one to six steps longer with the filter option of PAUP.

The *ndh*F sequences used here had several six to twelve base pair insertions or deletions (indels) inferred from gaps in the sequence alignments, which in previous analyses had been re-scored as binary characters and used as either an independent data set or combined with the sequence data (Scotland et al., 1995). These indels were viewed as having phylogenetic importance (Scotland et al., 1995); therefore indels found in the Gesneriaceae were removed and examined independently of sequence data for their phylogenetic utility.

The monophyly of various tribal relationships not obtained in the most-parsimonious trees was examined by using the constraints option of PAUP. These included the Trichosporeae, the Didymocarpeae, the inclusion of Klugieae in Cyrtandroideae, and Sinningieae in Gloxinieae. Also, since the analysis with all 16 outgroup taxa resulted in the placement of *Nematanthus* Schrader and Klugieae in discrepant positions from traditional classifications, an analysis with all 16 outgroups constrained *Nematanthus* to the Gesnerioideae, and the Klugieae from the Gesnerioideae. The position of Klugieae and *Nematanthus* was also examined by constructing a user-defined tree with a topology of one of the two most-parsimonious trees except that *Nematanthus* was placed in the Episcieae, and Klugieae was placed as sister to the remainder of the Gesneriaceae. This user-defined tree was then the

starting tree for a search using TBR and mulpars "on."

Results

Complete sequences for the *ndh*F gene were obtained for 52 species of Gesneriaceae (Table 1). These sequences were supplemented with sequences from an additional 18 species (2 within Gesneriaceae and 16 from related families) from Genbank (Table 1). The complete sequences resulted in 849 phylogenetically informative characters among all 70 species in the full analysis. A smaller analysis focused on only the Gesneriaceae species with *Paulownia* as the outgroup. Within this smaller analysis 690 nucleotide positions were found to be phylogenetically informative. Indels were found at several positions in the Gesneriaceae from the sequences used in this analysis. Two widespread insertions were a 12 bp insertion at position 1440 and a 6 bp insertion at 1548. Other insertions were autapomorphic for species or genera used in the analysis (unpublished results). No insertions were used in the analysis. The 6 bp insertion was symplesiomorphic for the Gesneriaceae. The 12 bp insertion was also symplesiomorphic for the Gesneriaceae; however, sequence divergence within this insertion provides an additional synapomorphy for the clade comprised of *Columnea*, *Drymonia* Mart., and *Alloplectus* Mart. (Fig. 4), where a single base pair transition characterizes these three genera. Other base pair substitutions and insertions were found within this 12 bp insertion but, with the current level of sampling, were autapomorphic.

Cladistic analysis was performed initially with all 70 taxa of the four families (Gesneriaceae, Scrophulariaceae, Acanthaceae, and Bignoniaceae) and all taxa in the three outgroup families designated as the outgroup. This analysis resulted in two trees of 5610 steps each (consistency index (CI) = 0.30, retention index (RI) = 0.48), all of which indicated the Gesneriaceae were a monophyletic family and that the genus *Paulownia* (Scrophulariaceae) was the closest outgroup (Figs. 1, 2).

Subsequent analyses were performed to minimize computer analysis time that utilized only the Gesneriaceae and *Paulownia* as a designated outgroup. This reduced analysis resulted in a single most-parsimonious tree of 4613 steps (CI = 0.27, RI = 0.38) (Figs. 3, 4). Some taxa that have been thought to be monophyletic, or comprised tribes, were examined using the constraints option of PAUP to determine the impact of the monophyletic grouping on the remainder of the data and to determine the number of additional steps required to construct these trees. The analysis required four additional steps to create a monophyletic Trichosporeae, five for a monophyletic Didymocarpeae, two to include the Klugieae in the Cyrtandroideae, and four to include the Sinningieae in the Gloxinieae. Constraining the analysis of all 70 taxa to place Klugieae as the sister to the Gesneriaceae and *Nematanthus* within the Episcieae resulted in four trees 58 steps longer than the most-parsimonious trees regardless of whether the constraint option of PAUP, or user defined trees were implemented.

Discussion

The cladistic analysis of 54 species of Gesneriaceae with 16 species of Scrophulariaceae, Bignoniaceae, and Acanthaceae as outgroups resulted in a monophyletic Gesneriaceae with the single genus *Paulownia* (Scrophulariaceae) indicated as the closest outgroup (Figs. 1, 2). These results verified that the Gesneriaceae are distinct from other members of the Lamiales s.l. and not an artificial unit based on their largely tropical distribution and herbaceous habit as has been seen for some family pairs (Judd et al., 1994). The full analysis is largely in agreement with the position of the taxa in the reduced analysis with the exception of the positions of *Nematanthus* and the tribe Klugieae. The placement of *Nematanthus* as the sister to the remainder of the family is very far removed from its traditional classification within the Episcieae (Fig. 1). Likewise the Klugieae are placed unusually in the subfamily Gesnerioideae (Fig. 2). The most likely explanation for the anomalous placement of these taxa is the high level of homoplasy between the Gesneriaceae and the outgroups. This is exemplified when 15 of the 16 outgroup species are removed from the analysis. In the reduced analysis both *Nematanthus* and Klugieae are in more expected positions regarding relationships to the remainder of the family. An alternative explanation is that because of the size of the data set, PAUP did not find the shortest tree and that a shorter tree with all 70 species exists that places *Nematanthus* and the Klugieae in their more expected relationships. This latter explanation is unlikely since searches constraining these taxa to their more traditional positions, or a user-defined tree that placed them there, resulted in four trees that were 58 steps longer.

The reduced analysis resulted in a single most-parsimonious tree (Figs. 3, 4). Three major monophyletic divisions within the family correspond to subfamilies Gesnerioideae and Cyrtandroideae (minus tribe Klugieae) and tribe Klugieae in a separate position as a potential third subfamily. Traditional

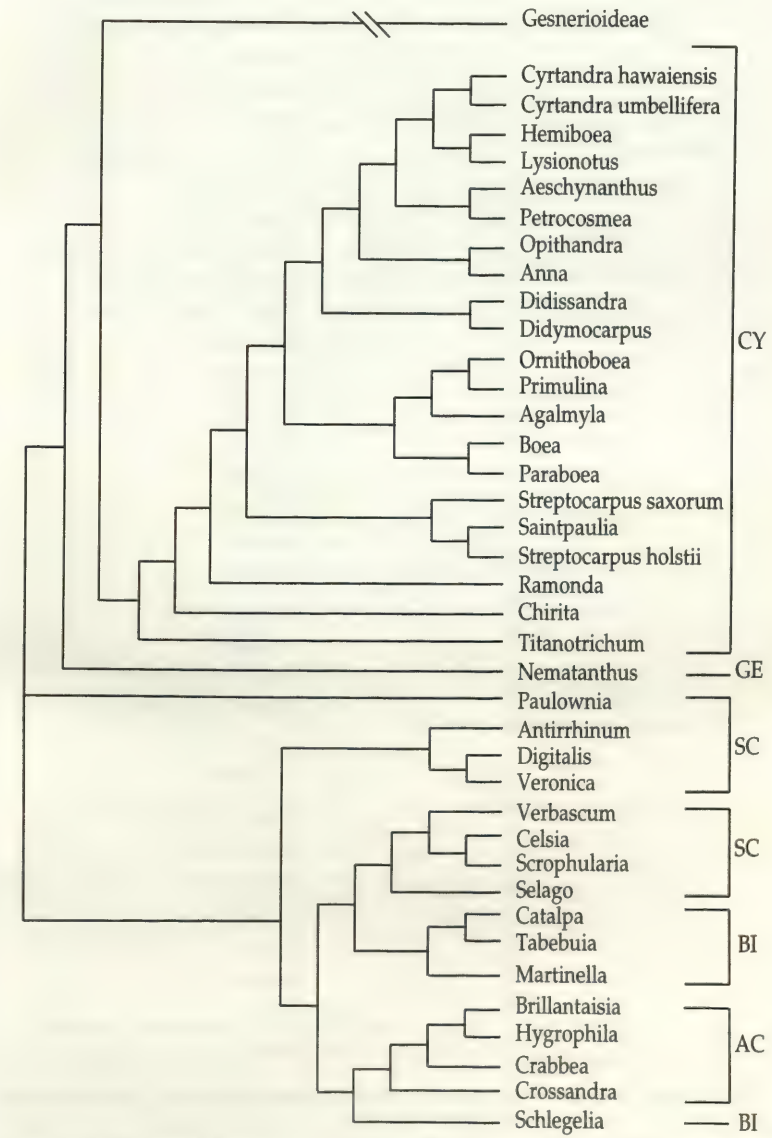


Figure 1. Strict consensus of two most-parsimonious trees of 5610 steps each (CI = 0.30, RI = 0.48) displaying the outgroup taxa, BI—Bignoniaceae, AC—Acanthaceae, SC—Scrophulariaceae, and the subfamilies of the Gesneriaceae, GE—Gesnerioideae and CY—Cyrtandroideae. The remainder of the Gesnerioideae are displayed in Figure 2. See text for explanation of position of *Nematanthus* in this cladogram.

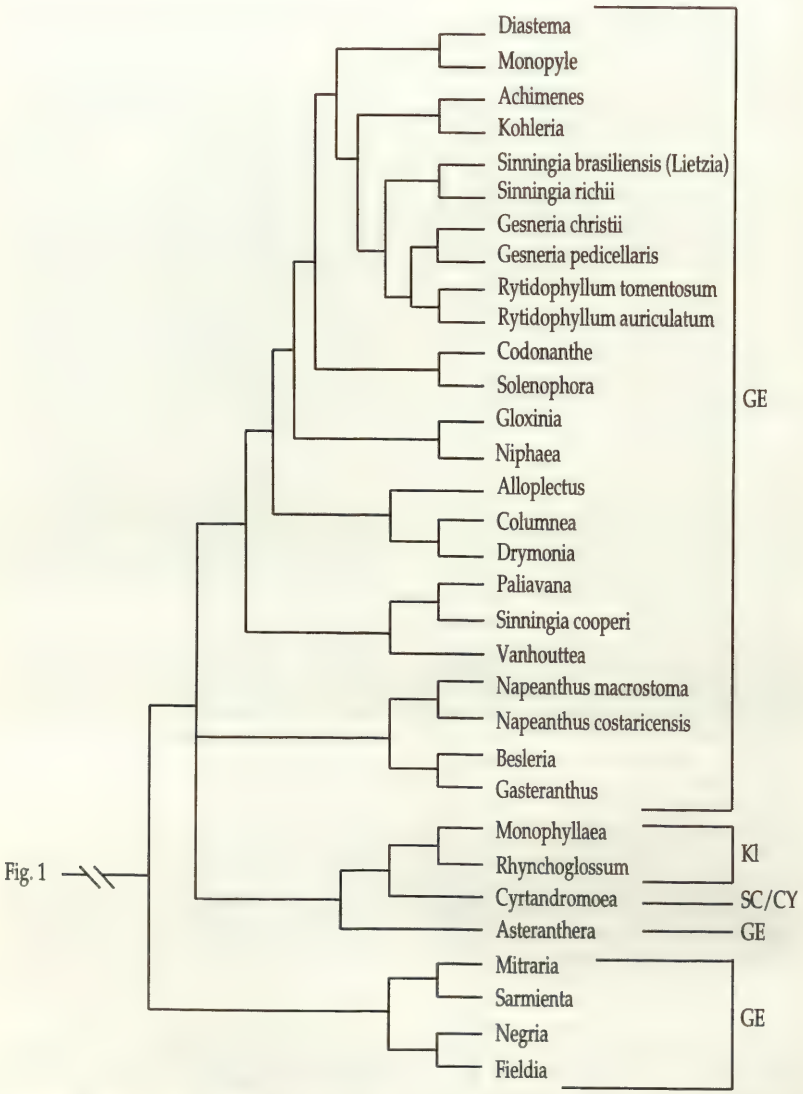


Figure 2. Strict consensus of two most-parsimonious trees of 5610 steps each (CI = 0.30, RI = 0.48) displaying the GE—Gesnerioideae, and some CY—Cyrtandroideae. *Cyrtandromoea* has been placed in either the SC—Scrophulariaceae or the Cyrtandroideae and is indicated as such on this figure. The remainder of the Cyrtandroideae are displayed in Figure 1. See text for the explanation of position of the tribe Klugieae (Kl) in this cladogram.

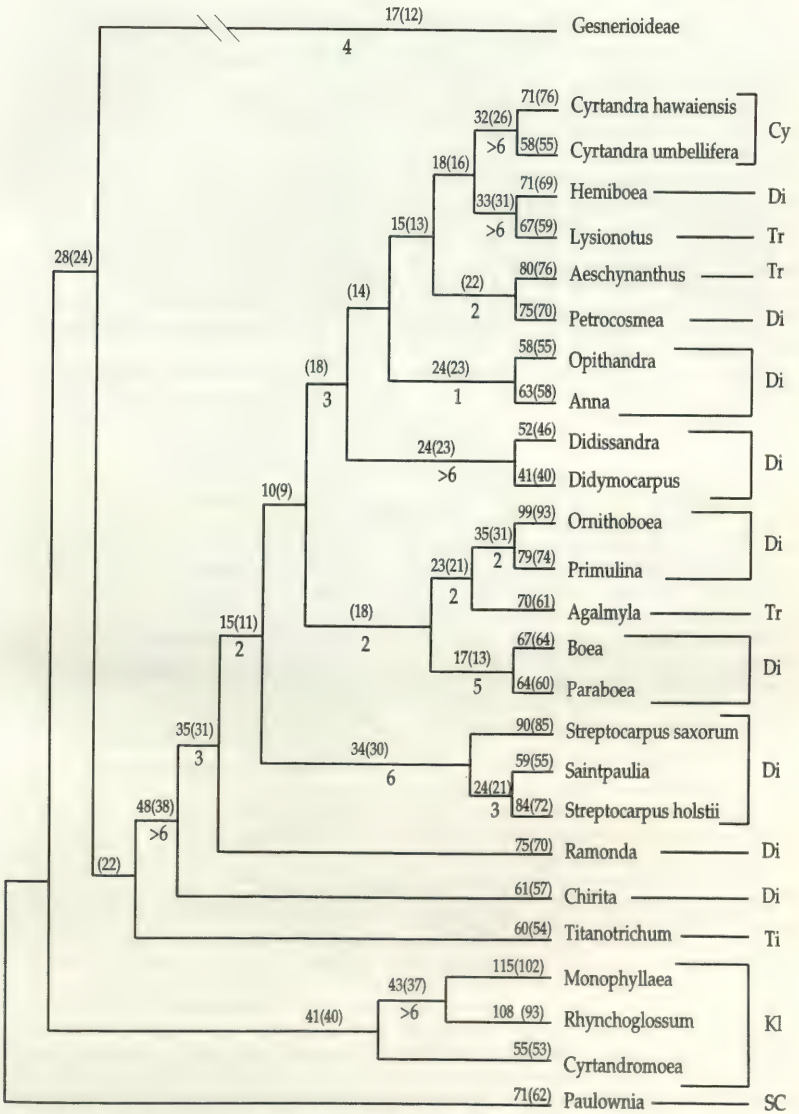


Figure 3. Single most-parsimonious tree of 4613 steps (CI = 0.29, RI = 0.38) from the analysis of the species in the Gesneriaceae with only *Paulownia* (SC—Scrophulariaceae) designated as the outgroup. Displayed in this figure are the tribes of the Cyrtandroideae, Kl—Klugieae, Ti—Titanotricheae, Di—Didymocarpeae, Tr—Trichosporeae, and Cy—Cyrtandreae. The Gesnerioideae are displayed in Figure 4. Numbers along branches are the synapomorphies that support those clades. Numbers in parentheses indicate those synapomorphies that are homoplastic in this tree. Numbers below branches are decay values. Branches with no value indicated have a decay value of 1.

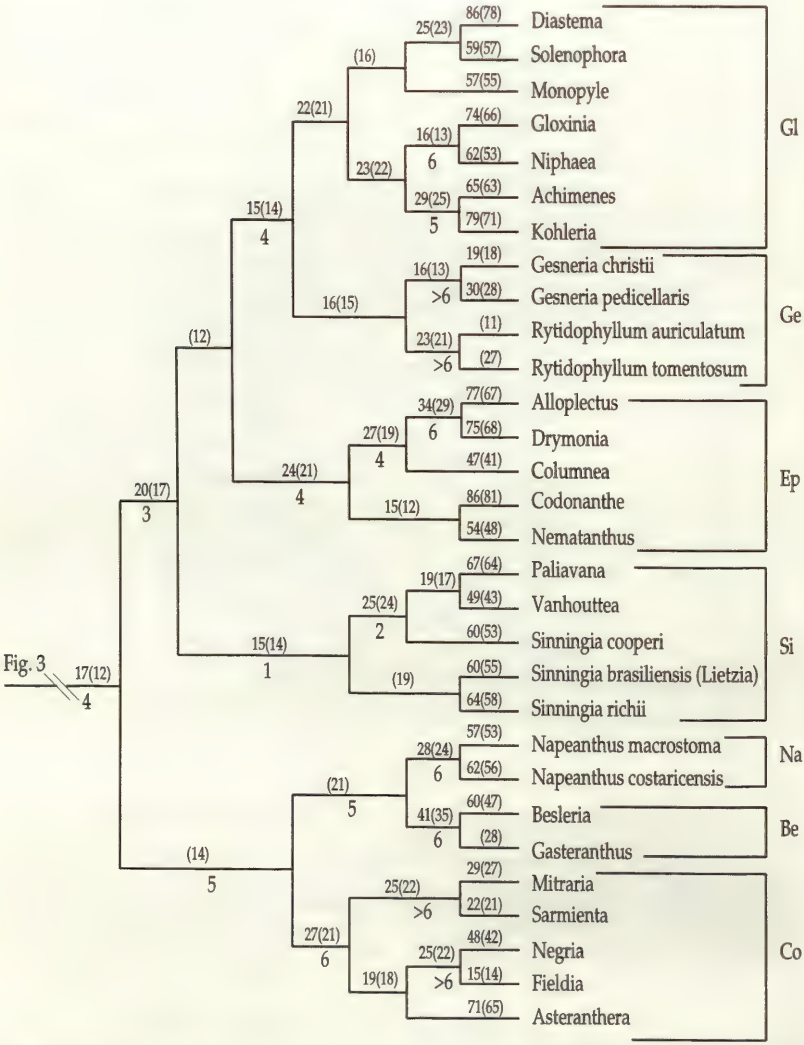


Figure 4. Single most-parsimonious tree of 4613 steps (CI = 0.29, RI = 0.38) from the analysis of the species in the Gesneriaceae with only *Paulownia* designated as the outgroup. Displayed in this figure are the tribes of the Gesnerioideae, Co—Coronanthereae, Be—Beslerieae, Na—Napeantheae, Si—Sinningieae, Ep—Episcieae, Ge—Gesnerieae, and Gl—Gloxinieae. The Cyrtandroideae are displayed in Figure 3. Numbers along branches are the synapomorphies that support those clades. Numbers in parentheses indicate those synapomorphies that are homoplastic in this tree. Numbers below branches are decay values. Branches with no value indicated have a decay value of 1.

classification schemes have placed tribe Klugieae in the Cyrtandroideae (Table 3); however, the inclusion of tribe Klugieae within subfamily Cyrtandroideae would result in a paraphyletic Cyrtandroideae. The removal of this tribe to a third subfamily would result in a monophyletic Cyrtandroideae. The monophyletic groups within the subfamily Gesnerioideae correspond highly with traditional classification systems for this subfamily (Wiehler, 1983) and a previous cladistic analysis based on morphological data (Smith, 1996). The relationships within the Cyrtandroideae are less congruent with previous taxonomic treatments, mainly due to the limited understanding and sampling of the large, heterogeneous tribe Didymocarpeae (Burtt, 1962).

SUBFAMILIAL GROUPINGS

The separation of the Gesneriaceae into two subfamilies (including Coronanthereae in the Gesnerioideae) has become well accepted during the past 30 years since the discovery of unequal cotyledon enlargement in the Cyrtandroideae (including members of the tribe Klugieae) and equal cotyledon enlargement in the Gesnerioideae (Burtt, 1962). However, from a cladistic viewpoint the Cyrtandroideae are defined by a synapomorphy whereas the Gesnerioideae are defined by a symplesiomorphy. One problem with this character is that it has not been examined thoroughly for all members of the different subfamilies, including many of the taxa used in this analysis.

Although an analysis of morphological data that included cotyledon expansion did not support the monophyly of the Cyrtandroideae (Smith, 1996), the cladistic analysis of *ndh*F sequences presented here demonstrates both a well-supported monophyletic Cyrtandroideae (Klugieae excluded) and Gesnerioideae (Figs. 3, 4). The monophyly of the Gesnerioideae is supported in both a morphological analysis (Smith, 1996) and this molecular analysis (Fig. 4). The Cyrtandroideae were paraphyletic in a cladistic analysis of morphological data (Smith, 1996) but are well supported with *ndh*F sequences (Klugieae excluded), although the position of *Titanotrichum* Solereder as sister to the remainder of the Cyrtandroideae is supported with only 22 homoplastic character state changes (Fig. 3).

The placement of Coronanthereae within the Gesnerioideae is well supported with *ndh*F sequences (Fig. 4) as it is with morphological data (Smith, 1996). This tribe does not belong in the subfamily Cyrtandroideae as had been proposed earlier (Fritsch, 1894). Wiehler (1983) in his treatment of the neotropical Gesneriaceae suggested a separate subfamilial status for Coronanthereae due to the numerous autapomorphic characters possessed by members of this group, such as fusion of the nectary to the ovary wall and high chromosome numbers (Wiehler, 1983). The morphological data would allow the Coronanthereae to be either a monophyletic tribe within the Gesnerioideae or a separate monophyletic subfamily without disrupting the taxonomy of any other group (Smith, 1996). However, based on the molecular data presented here, if the Coronanthereae were raised to subfamily level, it would either include the tribes Napeantheae and Beslerieae from the Gesnerioideae or necessitate elevating these two tribes as an additional subfamily (Fig. 4). Therefore it is recommended that the Coronanthereae be treated as a tribe of the Gesnerioideae rather than a separate subfamily.

TRIBAL RELATIONSHIPS
GESNERIOIDEAE

Among the relationships within the Gesnerioideae, the primary lack of congruence between this analysis and the most recent classification scheme by Burtt and Wiehler (1995) is the polyphyly of the Gloxinieae. However, the removal of *Sinningia* Nees (including *Lietzia* Regel, but not including *Paliavana* Vandelli or *Vanhouttea* Lem.) has been proposed previously (Fritsch, 1893, 1894) as the tribe Sinningieae. The monophyly of *Paliavana, Lietzia,* and *Sinningia* has been proposed by Boggan (1991), where all three genera were proposed to be members of *Sinningia* as the result of a morphologically based cladistic analysis of *Sinningia* species and several related genera. These results were not supported with a morphology-based cladistic analysis (Smith, 1996), most likely due to limited sampling among these taxa (*Sinningia* sensu stricto was represented only by *Sinningia* sect. *Corytholoma* and *Vanhouttea* was not included). The results presented here indicate that *Sinningia* (including the recently combined *Lietzia*), *Paliavana,* and *Vanhouttea* should be removed from Gloxinieae and placed in a separate monophyletic tribe Sinningieae. Although *Sinningia* is paraphyletic in this analysis (Fig. 4), limited sampling from this large genus leads only to a tentative conclusion that both *Paliavana* and *Vanhouttea* should be combined into *Sinningia* to create a monophyletic genus.

The sister relationship of the Beslerieae and Napeantheae has been hinted at based on the overlap of several diagnostic characters between these tribes (Skog, 1995; Skog & de Jesus, 1996). However, the sister relationship of these two tribes to

the Coronanthereae (Fig. 4) has not been proposed previously. Although the morphological data did not indicate sister group status, the data did indicate a close affinity among these three tribes (Smith, 1996).

Among the recent classification schemes proposed for the Gesnerioideae, Burtt and Wiehler's (1995) is the closest approximation to the results obtained in this study. The subdivision of Wiehler's (1983) Gloxinieae into the Bellonieae, Kohlerieae, Rechsteinerieae, and Solenophoreae (Ivanina, 1965) (Table 2) is not supported by this cladistic analysis. Likewise separating Wiehler's (1983) Gloxinieae into Bellonieae, Kohlerieae, and Solenophoreae (Table 2; Fritsch, 1893, 1894) is not supported except for the removal of the Sinningieae (Fig. 4), which would also necessarily include *Paliavana* and *Vanhouttea* (included in Fritsch's Kohlerieae; Table 2). The placement of *Napeanthus* G. Gardner in the Klugieae (Cyrtandroideae) (Table 2) as proposed by Fritsch (1893, 1894) is inappropriate.

CYRTANDROIDEAE

Burtt's (1962, 1977) classification system for the Cyrtandroideae is closer in agreement to this cladistic analysis than previous classification schemes (Ivanina, 1965; Fritsch, 1893, 1894). However, the monophyly of the largest tribe, the Didymocarpeae, is not supported by this analysis (Fig. 3). Likewise none of the subtribes created by Ivanina (1965) or Fritsch (1893, 1894) are supported as monophyletic groups (Fig. 3, Table 3). The Trichosporeae are not supported as a monophyletic clade (Fig. 3). Although this tribe was well supported in the morphological analysis (Smith, 1996), four additional steps beyond the most-parsimonious tree are required to make this clade monophyletic with *ndh*F data.

The position of *Titanotrichum* has been problematic, although this genus has consistently remained in the Gesneriaceae (Burtt, 1962, 1977; Wang et al., 1992; Burtt & Wiehler, 1995). *Titanotrichum* is a member of the Cyrtandroideae based on these data, and perhaps may be viewed best as a monotypic tribe (Titanotricheae; Wang et al., 1992), sister to the remainder of the subfamily. However, the position of *Titanotrichum* as the sister to the remainder of the Cyrtandroideae is only weakly supported with 22 homoplastic character state changes, and the resolution of its placement is lost in the strict consensus of all trees only one step longer than the most-parsimonious tree. Therefore, it is likely that *Titanotrichum*, or the lineage leading to this species, diverged early in the evolution of the family. The placement of *Titanotrichum* within the Gesneriaceae is discussed elsewhere (Smith et al., 1997).

The Didymocarpeae are a large heterogeneous tribe that includes the majority of genera in the Cyrtandroideae (Burtt, 1962, 1977; Wang et al., 1992). In this analysis it is a paraphyletic assemblage that includes the Cyrtandreae and Trichosporeae (Figs. 1, 3). Because of the large size of the Didymocarpeae, and the limited sampling of the tribe in this analysis, no conclusions regarding its monophyly, or potential division into other tribes, are recommended at this time. Further morphological investigations in this tribe are under way (B. L. Burtt and A. Weber, pers. comm.), and a cladistic analysis that focuses on this group will be valuable toward understanding its relationships. Several well-supported monophyletic groups within the Didymocarpeae can be identified (*Boea* Commerson ex Lamarck/*Paraboea* (C. B. Clarke) Ridley, *Hemiboea* C. B. Clarke/*Lysionotus* D. Don, *Didissandra* C. B. Clarke/*Didymocarpus* Wallich, and *Streptocarpus* Lindl./*Saintpaulia*). It should be noted that *Didissandra* and *Didymocarpus*, although forming a monophyletic clade in this analysis, are both large heterogeneous genera and that sampling different species may have resulted in different placement. By focusing on morphological characters of these groups it may be possible to identify more inclusive monophyletic tribes out of the paraphyletic Didymocarpeae. Much greater sampling within this large group will be necessary before any major realignment can begin.

An unexpected result of this analysis is the paraphyly of *Streptocarpus*. The most likely explanation for this paraphyly is limited sampling, with only two species of *Streptocarpus* and one of *Saintpaulia*. However, it is interesting to note that *Saintpaulia* is one of the few genera within the Gesneriaceae to have a chromosome number of $n = 15$ (Skog, 1984). The only other genera that share this number are some species of *Streptocarpus*, including both *S. saxorum* and *S. holstii*, and some species of *Aeschynanthus* Jack (Skog, 1984). The possibility that *Saintpaulia* is derived from within *Streptocarpus*, as indicated by *ndh*F sequences and chromosome numbers, currently is being investigated with greater sampling.

The Trichosporeae traditionally have been viewed as a monophyletic tribe defined by the presence of seed appendages not present elsewhere within the family (Burtt, 1962, 1977; Wang et al., 1992). Based on morphological data, the Trichosporeae were one of the most strongly supported

tribes in a morphology-based cladistic analysis (Smith, 1996). However, it is apparent from this analysis of *ndh*F sequences that the selection of characters that define the Trichosporeae is inappropriate (e.g., seed appendages are common in the closely related Bignoniaceae). Alternatively, it is possible that inadequate sampling from the Trichosporeae or the large tribe Didymocarpeae may be causing the separate placement of the three genera sampled from the Trichosporeae. This latter hypothesis is unlikely, because one of the more strongly supported clades in the analysis placed *Lysionotus* (Trichosporeae) with *Hemiboea* (Didymocarpeae) and away from the other genera of the Trichosporeae (Fig. 3).

KLUGIEAE

The Klugieae are monophyletic and are the sister group to the remainder of the Gesneriaceae (Fig. 3). The placement of this tribe in the Gesnerioideae (Fig. 2) in the full data analysis most likely is due to homoplasy or the result of an incomplete search for the shortest tree. The monophyly and sister group status of this tribe also was supported with a cladistic analysis of morphological data (Smith, 1996). The Klugieae possess numerous autapomorphic characters relative to other Gesneriaceae such as narrow medullary rays, and verrucate edges of the cells of the seed coat (Smith, 1996). The placement of *Cyrtandromoea* Zoll. in the Klugieae of the Cyrtandroideae was proposed previously by Ivanina (1965), although other investigations indicated that this genus should be excluded from the Gesneriaceae on the basis of floral anatomy (Burtt, 1965; Singh & Jain, 1978). The placement of *Cyrtandromoea* in the Gesneriaceae is discussed elsewhere (Smith et al., 1997).

EVOLUTION OF NON-MOLECULAR CHARACTER STATES

CHROMOSOME NUMBERS

Several chromosome counts are synapomorphic and non-homoplastic based on this cladistic analysis. Large numbers of chromosomes ($n = 30+$) are unique to the Coronanthereae and would serve as an additional character to separate this tribe from the remainder of the family (Skog, 1984). A chromosome base number, x, of 14 characterizes the Gesnerieae (Wiehler, 1983; Skog, 1984). The cladistic analysis of morphological data was unable to separate the Gesnerieae from the tribe Gloxinieae although it represented a monophyletic group within it (Smith, 1996). The inclusion of chromosome numbers (which were excluded due the large number of character states) might have removed Gesnerieae from Gloxinieae as seen here with sequence data.

Most Gloxinieae sampled here (excluding *Solenophora* Benth., *Niphaea* Lindl., and *Achimenes* Pers.) have $x = 13$ (Wiehler, 1983; Skog, 1984). In addition, the members of the Sinningieae that have been examined also have $x = 13$ (Skog, 1984). This similarity in chromosome base number, along with other character states, has led previous researchers to include the members of the Sinningieae within the Gloxinieae (Wiehler, 1983). However, based on the analysis presented here, the Sinningieae are best viewed as a tribe separated from the Gloxinieae, and $x = 13$ is homoplastic.

Other homoplastic chromosome numbers are $x = 11$ (*Niphaea* and *Achimenes*), and $x = 9$ (*Alloplectus, Drymonia, Columnea,* and some *Didymocarpus* species). Although most of these homoplastic counts serve little phylogenetic utility, the count of $x = 9$ serves to characterize a portion of the Episcieae. Most members of the Episcieae have $x = 9$, but taxa with $x = 8$ (*Codonanthe* (Mart.) Hanst. and *Nematanthus*) may represent another clade (Fig. 4). Further sampling within the Episcieae may reveal if this clade (Fig. 4) continues to be supported or is the result of sampling in this analysis.

Other chromosome counts in the Cyrtandroideae are highly variable even within genera, and no pattern emerges from the counts of the species that have been included in the analysis, with the exception of the *Streptocarpus*/*Saintpaulia* counts discussed above.

NODAL ANATOMY

Another useful character for the Gesneriaceae is nodal anatomy (Wiehler, 1983). Unfortunately only the subfamily Gesnerioideae has been sampled thoroughly for this character, and the lack of data for the Cyrtandroideae necessitated the exclusion of this character from the morphological analysis (Smith, 1996). However, if nodal anatomy is mapped onto the trees from this molecular analysis, this character can provide useful phylogenetic information. The tribe Episcieae (Fig. 4) is defined by a three-trace trilacunar node that is unique among the Gesnerioideae, although this character state is known from the Cyrtandroideae. The unique presence of this character state within the Gesnerioideae adds further support to the monophyly of the Episcieae. The three-trace trilacunar node may be symplesiomorphic for the Cyrtandroideae, as all taxa with available data for this character (*Saintpaulia, Streptocarpus,* and *Cyrtandra* Forster & Forster) possess a three-trace trilacunar node except

Aeschynanthus, which has a one-trace trilacunar node common to the Gesnerioideae.

PLACENTA

The placenta in the Gesneriaceae is either intact or divided to the base (Ivanina, 1965). This character was included in a cladistic analysis of morphological data and served as a character state that brought the Episcieae, Beslerieae, and Napeantheae together in a single clade (Smith, 1996) as the only taxa sampled that had divided placentae. Although this character state is consistent with the relationship between the Napeantheae and Beslerieae, the character state is homoplastic between the Episcieae and Napeantheae/Beslerieae based on the data presented here (Fig. 4).

STEM MODIFICATION

Several members of the Gesneriaceae possess modifications of the stems (rhizomes and tubers), presumably as adaptations to periodic dry seasons (Wiehler, 1983). The presence of scaly rhizomes is found almost exclusively, and is widespread, within the Gloxinieae (Wiehler, 1983). Among the taxa sampled here, the presence of scaly rhizomes serves as a synapomorphy for the tribe Gloxinieae, although they are not known from the woody genus *Solenophora*. Scaly rhizomes also are known from the Cyrtandroideae, including *Titanotrichum* (Kao & DeVol, 1972; Wang et al., 1992).

Tubers are widespread among species of *Sinningia* including *Lietzia*, which has recently been combined into *Sinningia* (Wiehler & Chautems, 1995). Although tubers serve to unite these genera, and to separate them from the Gloxinieae, tubers are not known from *Paliavana* or *Vanhouttea*. However, not all species of *Sinningia* are tuberous, and the lack of tubers in these species can be regarded as intratribal or intra-generic variation. Tubers also are known from several species in the Episcieae (*Drymonia*, *Chrysothemis* Dcne., *Nautilocalyx* Lind. ex Hanst., *Paradrymonia* Hanst., and *Rhoogeton* Leeuwenberg) as well as one member of the Gloxinieae (*Lembocarpus* Leeuwenberg). Further studies that include these taxa will hopefully resolve the number of times tubers have originated within the Gesneriaceae.

BIOGEOGRAPHY

The traditional division of the Gesneriaceae into two subfamilies (excluding the Klugieae, which may stand best as a third subfamily) is well supported in this analysis and is in agreement with the biogeographic distribution of these taxa. The Cyrtandroideae (excluding the Klugieae) are distributed almost exclusively in the paleotropics with a few temperate European and Asian species. Two African genera were included in this analysis, both of which are in a single clade (*Saintpaulia* and *Streptocarpus*). Only one of the European taxa (*Ramonda* L. C. Richard) has been included in this analysis; therefore nothing can be inferred regarding the origin of these taxa at this time.

Members of the tribe Klugieae range from India to south China, Taiwan, the Philippines through Malaysia, Indonesia, and into New Guinea. Discrepancies from this distribution include a single species of *Rhynchoglossum* Blume found in Central and South America. The presence of *Rhynchoglossum azureum* (Schlecht.) B. L. Burtt in the Neotropics represents a secondary dispersal event in the family, because all other members of the Klugieae are found in the Old World.

The Gesnerioideae are almost exclusively neotropical, but with the inclusion of the Coronantheae within this subfamily the Gesnerioideae now encompass several Australian and South Pacific island species.

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A PHYLOGENETIC CONSPECTUS OF THE TRIBE JUANULLOEAE (SOLANACEAE)[1]

Sandra Knapp[2], *Viveca Persson*[2], *and Stephen Blackmore*[2]

ABSTRACT

The tribe Juanulloeae has traditionally consisted of nine genera of rarely collected, epiphytic shrubs and small trees: *Juanulloa, Markea, Schultesianthus, Trianaea, Dyssochroma, Hawkesiophyton, Rahowardiana, Ectozoma,* and *Merinthopodium.* Here we present the results of a cladistic study of the relationships of the species of these genera and provide a conspectus of the genera as we define them. The number of genera in our treatment is reduced to six: *Dyssochroma, Juanulloa, Markea, Merinthopodium, Schultesianthus,* and *Trianaea.* Included in the key and conspectus is the genus *Solandra,* which at present is treated as a separate tribe, Solandreae. We also discuss the groupings on the tree and point out areas for future research in this group. A key to the genera is provided and for each genus a list of component taxa and their distributions is also given. Many of these genera have previously been illustrated, but illustrations are provided for some of the previously unillustrated taxa or for taxa where illustrations are difficult to find.

The Solanaceae are an economically important, cosmopolitan family with over 2500 species that have traditionally been divided into two subfamilies. The Cestroideae, including petunias, the cestrums and their relatives, have non-compressed, often prismatic seeds and tropane alkaloids. The Solanoideae, which contain the large majority of the species in the family, include *Solanum* and its relatives that have compressed seeds and steroidal alkaloids. This traditional classification has recently been challenged by cladistic analyses using chloroplast and nuclear DNA data sets, and the family can now be divided into approximately seven monophyletic groups (see Olmstead et al., in press).

The tribe Juanulloeae, first described by Hunziker (1977), is placed in the subfamily Solanoideae in both the traditional and phylogenetic systems: its members share flat, discoidal seeds and curved embryos with others in that subfamily. The tribe as defined by Hunziker (1977, 1979) is delimited by a combination of habit, anther, and seed characters and consists of nine genera: *Dyssochroma* Miers, *Ectozoma* Miers, *Hawkesiophyton* Hunz., *Juanulloa* Ruiz & Pavón, *Merinthopodium* Donn. Sm., *Markea* Rich., *Rahowardiana* D'Arcy, *Schultesianthus* Hunz., and *Trianaea* Planch. & Linden. The Juanulloeae are thought to be closely related to the genus *Solandra* Swartz, the only member of the Solandreae. *Trianaea* was previously considered a member of the Solandreae (Hunziker, 1979; Bernardello & Hunziker, 1987), but was transferred to the Juanulloeae (Hunziker & Bernardello, 1989) owing to its ex-endospermous seeds and almost straight embryos with oblique, accumbent cotyledons. *Solandra* differs from the members of the Juanulloeae in its incumbent rather than accumbent cotyledons and its partially inferior ovary (D'Arcy, 1973 [1974]). Miers (1857) allied *Solandra, Juanulloa, Markea, Sarcophysa* Miers (*Juanulloa speciosa* (Miers) Dunal), and *Dyssochroma* as the Solandreae, which he considered to be closely related to the shrubby neotropical genus *Brunfelsia* L. *Brunfelsia* is now considered to be related either to *Salpiglossis* L. and its relatives (Hunziker, 1979) or to *Petunia* L. (Olmstead et al., in press). In the recent molecular phylogeny of the family Juanulloinae and Solandrinae are united in the tribe Juanulloeae (see Olmstead et al., in press). The general habit and morphological similarities of the Juanulloeae and *Solandra* have long been recognized and we have thus included *Solandra* in this analysis.

The genera of the Juanulloeae (here referred to in the broad sense, including *Solandra*) are all neotropical, epiphytic trees and shrubs. Many of the species are myrmecophilous, especially in the ge-

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[2] Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom.

Figure 1. *Markea formicarum* Dammer. Specimen illustrating the swollen ant-inhabited stem-bases (*Nee 30923*, NY).

nus *Markea*, where two Amazonian species are associated with particular species of ants (Ducke, 1915: *M. camponoti* Ducke associated with *Camponotus femoratus* (F.) and *M. formicarum* Damm. with *Azteca* sp.). Species of *Hawkesiophyton* (here treated as congeneric with *Markea*) are often associated with various species of ants (Ducke, 1922), and seedlings of *M. panamense* Standl. produce enlarged basal stems even in the absence of ants (Garwood, pers. comm.). The swollen tuber-like stems and roots seen in these species (Fig. 1) are often hollow and are probably used by ants for nests and storage. In some ant plants, a mutualistic relationship exists between the insect and the plant, with high percentages of both carbon and nitrogen being derived from ant respiration and debris deposition (Treseder et al., 1995).

Some members of the Juanulloeae are fed upon by the larvae of the Ithomiinae (Lepidoptera: Nymphalidae), specialist herbivores of the family Solanaceae. *Solandra, Schultesianthus, Markea, Juanulloa,* and *Merinthopodium* are fed upon by larvae of the genera *Olyras, Eutresis,* and *Melinaea* (tribe Melinaeini), which are all high flying canopy dwell-

Figure 2. —A. *Juanulloa mexicana* (Schltdl.) Miers, cult. Royal Botanic Gardens, Kew, scale bar = 1.5 cm.—B. *Solandra maxima* Sessé & Mociño, cultivated, University of Texas, Austin, TX, originally collected at Las Tuxtlas, Veracruz, Mexico (photo J. Mallet), scale bar = 4 cm.

Figure 3. —A. *Merinthopodium neuranthum* (Hemsl.) Donn. Sm., fallen flower post-anthesis; note the broadly campanulate shape (Monteverde, Costa Rica), scale bar = 2 cm.—B. *Trianaea speciosa* (Drake) Soler., *Knapp et al. 9121*, Loja–Zamora road, Ecuador, scale bar = 2 cm.

ers (for a complete listing of the host plant relationships of these butterflies see Drummond & Brown, 1987). The young larvae make characteristic "C"-shaped damage in the leaves, but have rarely been reared and are difficult to collect from the forest canopy.

In common with many other tropical epiphytes the leaves of species in the group tend to be thick and leathery, and the branches flexible with pliable bark. Flower shape in the Juanulloeae varies considerably from the long, red or bright orange, presumably hummingbird-pollinated, flowers of *Markea coccinea* Rich. and most of the species of *Juanulloa* (Fig. 2A) to the greenish, open campanulate flowers of the species of *Trianaea* (Fig. 3B), *Merinthopodium* (Fig. 3A), and *Dyssochroma*, which are bat-pollinated (Voss et al., 1980). In every case, apart from *Markea panamensis*, however, the flowers are sympetalous and have relatively long corolla tubes. Fruits of members of the Juanulloeae are generally fleshy to leathery berries, with some variation in the thickness of the berry wall. Genera of the tribe have been traditionally delimited (Hunziker, 1977, 1979) using combinations of the following characters: insertion of the anthers on the filaments, filament insertion on the corolla tube, and corolla aestivation. Characters and their states are discussed more fully in Materials and Methods.

Few collections are known for most of the species and this makes the assessment of characters difficult since the extent of variability is not known. Woody tropical epiphytes are difficult to collect as they often grow high in the canopy and flower only rarely. Many of the species of the Juanulloeae are known only from flowering material, and thus decisions based on fruit characters tend to be rather ad hoc at best. With few specimens available it is nearly impossible to assess variability in characters, and a tendency to overdivide at the generic level is apparent and understandable.

Recent applications of molecular systematics have been extremely useful in providing broad frameworks for directing future study. However, at present, the limited range of taxa that has been

Table 1. Taxa used in the cladistic analysis. Names in parentheses are those used in Persson et al. (1994).

Nicandra physalodes (L.) Gaertner
Atropa belladonna L.
Lycium cestroides Schltdl.
Dyssochroma longipes (Sendtner) Miers
Dyssochroma viridiflora (Sims) Miers
Juanulloa ferruginea Cuatrecasas
Juanulloa globifera (S. Knapp & D'Arcy) S. Knapp (*Rahowardiana globifera*)
Juanulloa membranacea Rusby
Juanulloa mexicana (Schltdl.) Miers
Juanulloa ochracea Cuatrecasas
Juanulloa parasitica Ruiz & Pavón
Juanulloa parviflora (Ducke) Cuatrecasas
Juanulloa pavonii (Miers) Benth. & Hook. (*Ectozoma pavonii*)
Juanulloa speciosa (Miers) Dunal
Juanulloa verrucosa (Rusby) Hunz.
Juanulloa wardiana (D'Arcy) S. Knapp (*Rahowardiana wardiana*)
Markea camponoti Ducke
Markea coccinea Rich.
Markea costanensis Steyerm.
Markea formicarum Ducke
Markea panamensis Standl. (*Hawkesiophyton panamense*)
Markea sessiliflora Ducke
Markea ulei (Dammer) Cuatr. (*Hawkesiophyton ulei*)
Markea lopezii Hunz.
Markea aff. *lopezii*
Merinthopodium neuranthum (Hemsl.) Donn. Sm.
Merinthopodium pendulum (Cuatr.) Hunz.
Schultesianthus coriaceus (Kuntze) Hunz.
Schultesianthus crosbianus (D'Arcy) S. Knapp (*Markea crosbiana*)
Schultesianthus dudleyi Bernardello & Hunz.
Schultesianthus leucanthus (Donn. Sm.) Hunz.
Schultesianthus megalandrus (Dunal) Hunz.
Schultesianthus odoriferus (Cuatr.) Hunz.
Schultesianthus uniflorus (Lundell) S. Knapp (*Markea uniflora*)
Schultesianthus venosus (Standl. & C. V. Morton) S. Knapp (*Markea venosa*)
Solandra brachycalyx Kuntze
Solandra boliviana Britton
Trianaea brevipes (Cuatr.) S. Knapp (*Trianaea spectabilis* var. *brevipes*)
Trianaea naeka S. Knapp (*Trianaea* sp. 1)
Trianaea neovisae Romero-Castañeda
Trianaea nobilis Planch. & Linden
Trianaea speciosa (Drake) Soler.
Trianaea sp. nov. (*Trianaea* sp. 4)

sampled makes direct comparison of these results to those from morphological studies difficult. The sampling of morphological characters is often more complete in any given group, especially at the family level, and thus relationships are more resolved. This is certainly true for this analysis of the Juanulloeae. The molecular analyses of Solanaceae undertaken to date have indicated a close relationship among *Juanulloa*, *Dyssochroma*, *Hawkesiophyton* (= *Markea*), and *Solandra* (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press). However, in those analyses only four species were sampled, thus somewhat limiting their usefulness at resolving relationships among genera or in determining whether or not the genera as presently defined are monophyletic.

This paper presents a cladistic analysis of the Juanulloeae based on macro- and micromorphological characters. It extends an earlier analysis that emphasized palynological characters (Persson et al., 1994) and provides a conspectus of the genera and species.

Materials and Methods

Taxa used in the cladistic analysis are listed in Table 1. By using species as terminal taxa we hoped to test the monophyly of genera in the group as presently defined. Nomenclatural changes necessitated by the results of this study were made in Knapp (1995), and the new combinations are used here. The names used in Persson et al. (1994) did not reflect these nomenclatural changes and thus are slightly different. Names in parentheses in Table 1 are those used in Persson et al. (1994) when a new combination is used here. Morphological characters were assessed using herbarium specimens from BM, CUVC, F, JAUM, K, MO, NY, and QCNE, and voucher specimens are cited in the appendix. Palynological characters were assessed as described in Persson et al. (1994), and pollen slides have been deposited in the collections at BM.

The cladistic analyses were performed using the computer program Hennig86 (Farris, 1988) using the *mhennig** option for the initial selection of most parsimonious trees, then *bb** for finding equally parsimonious trees. These options are recommended for use with large data sets where exhaustive iteration can be prohibitively time-consuming for finding shortest trees (Farris, 1988), and have been shown to be as good as the *ie* option in many test data sets (Platnick, 1989). The ensemble consistency index (CI) is a measure of homoplasy in the data set with respect to the fit of characters to the tree. When the fit of a character is perfect (with no parallelism or reversal) then the consistency index equals 1. The ensemble retention index (RI) is the fraction of apparent synapomorphy in a character that is retained as synapomorphy on the tree (Far-

ris, 1989). Trees were also constructed using NONA (Goloboff, 1993) to confirm the actual versus potential groupings on the tree, as NONA and Hennig86 treat zero length branches (potential groupings) in a different way. The following commands, as recommended by Goloboff (1993), were used: hold 100, hold/20, and mult*50.

Successive approximation weighting (*xs w* option in Hennig86) was used to assess the reliability of fit of characters to the most parsimonious tree. The fitting function in the MS-DOS program PeeWee (Goloboff, 1993) was also used to assess character reliability. Character weighting, when applied to the fit of characters, emphasizes those characters that best fit the initial tree topology. Successive weighting allows the characters to judge themselves in terms of their reliability: i.e., their best fit to the solution supported by all the data (Carpenter, 1994). Best fit is judged by the shortest tree (Farris et al., 1970), the shortest tree for the weighted data in terms of tree length (Farris, 1969), or the "heaviest" tree when calculated as a function of character weights (Goloboff, 1993). Characters that are more homoplasious are less reliable and are thus downweighted in these analyses. Successive weighting (Hennig86, *xs w* option) uses the rescaled consistency index (rc) of Farris (1989) as the weighting function of each character: it is calculated as the product of ensemble RI (retention index) times ensemble CI (consistency index) and scaled between 0 and 10. Goloboff (1993) calculates weights as the extra number of steps per character such that the weight = K/K+ESi, where ESi is the extra steps per character and K is the concavity constant (in our analyses set at K = 3).

The characters were coded to be unordered, thus minimizing ad hoc weighting or polarity before analysis. In this analysis we used 43 taxa and 38 characters (Table 2). Three taxa were selected as outgroups (see Tables 1 and 3), *Nicandra physalodes*, *Atropa belladonna*, and *Lycium cestroides*, representing a range of putative sister taxa for the Juanulloeae. Choosing a range of outgroups (Watrous & Wheeler, 1981) has been thought to increase the likelihood of obtaining an accurately rooted tree. Recent work, however (Nixon & Carpenter, 1993), has shown that multiple outgroups perform no better at "polarizing" ingroup nodes, but that multiple outgroups might improve inference. One difference in this data set from that used in Persson et al. (1994) is the omission of *Mandragora* as one of the outgroups for the analysis. Olmstead and Palmer (1992) had originally identified *Mandragora* and *Solandra* as sister taxa using chloroplast DNA restriction site mapping. More recent work has revealed that *Mandragora* is an isolated taxon of uncertain affinity, possessing many autoapomorphies, both molecular (Olmstead & Sweere, 1994; Olmstead, pers. comm.) and morphological.

Table 2. Characters used in the cladistic analysis of the Juanulloeae.

0. Habit shrubs 0, herbs 1, epiphytes 2.
1. Peltate glandular trichomes on leaf surfaces absent 0, present 1.
2. Inflorescence of solitary flowers 1, few flowers 0, many flowers 2.
3. Inflorescence axis condensed 0, elongate 1.
4. Calyx lobes shorter than the corolla tube 0, equal to the corolla tube 1.
5. Calyx texture at anthesis membranous 0, coriaceous 1.
6. Calyx lobes acute 0, acuminate 1, long-acuminate 2, rounded 3.
7. Flowers radially symmetric 0, zygomorphic 1.
8. Corolla aestivation overlapping 0, valvate 1.
9. Flower shape narrow tube 1, salverform 2, open 0, campanulate 3.
10. Corolla color green/white 0, purple-purplish green 1, red, orange, or yellow 2.
11. Filaments straight 0, declinate 1.
12. Filament tube absent 0, present 1.
13. Filament base glabrous 0, pubescent 1.
14. Filament base pubescence dense 0, sparse 1.
15. Filaments inserted in anther basally 0, dorsally 1, ventrally 2.
16. Anthers included in the corolla tube 1, at mouth of corolla tube 0, exserted 2.
17. Anthers dehiscing separately 0, confluently 1.
18. Ovary superior 0, partially inferior 1.
19. Ovary ± conical 0, narrowly beaked 1.
20. Fruit pericarp membranous 0, coriaceous 1.
21. Seeds reniform 0, rectangular 1.
22. Cells in center of testa square 0, elongate 1.
23. Lateral cell walls straight 0, sinuate 1.
24. Dried seed color pale brown 0, dark brown 1, orange 2.
25. Undigested seed surface pitted 0, smooth 1.
26. Spiny supratectal processes absent 0, present 1.
27. Colpi extending nearly to the poles 0, relatively short 1.
28. Pollen without Ubisch bodies 0, covered with Ubisch bodies 1.
29. Colpi with continuous margins 0, lalongate apertures 1.
30. Exine around apertures thickened 0, not thickened 1.
31. Tectum continuous 0, not continuous 1.
32. Beak-like margo apertures absent 0, present 1.
33. Colpus border not thickened 0, thickened 1.
34. Outline in equatorial view spherical 0, oblate 1.
35. Outline in polar view obtuse, convex 0, acute, straight 1.
36. Nexine same thickness as the sexine 0, nexine thicker than the sexine 1.

The data matrix is presented in Table 3. Most of the characters are self-explanatory; those peculiar to the Juanulloeae are described in detail here and the palynological characters were discussed in

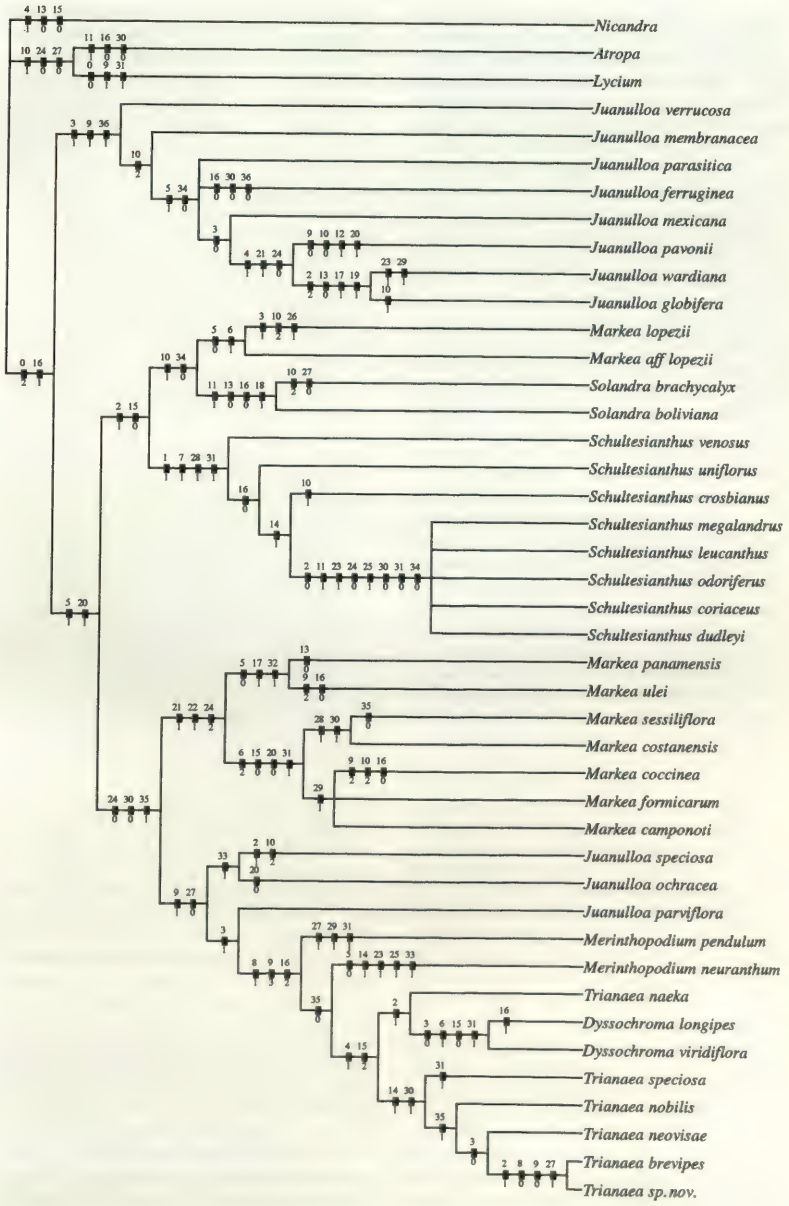
Table 3. Data matrix used for the analysis of the Juanulloeae.

Nicandra	100010000000?0200000001001001000100
Atropa	100000000011010100000000000000000100
Lycium cestroides	000000000110010120000000000000001100100
Solandra brachycalyx	201001000021 00?000101000100000010000000
Solandra boliviana	20100100001100?000101?????01001000000
Markea sessiliflora	200001200000010010000110200110110100
Markea costanensis	20000120000001001000?????01101100110
Markea coccinea	200001200220010000000110200101010011 0
Markea formicarum	200001200000010010000110200101010011 0
Markea camponoti	200001200000010010000110200101010011 0
Markea lopezii	201100100020010010 00??????11001000000
Markea aff. lopezii	201000100010010010 00????????????????
Markea panamensis	200000000000?1110011102001000010110
Markea ulei	200000000200010101001110200100010110
Merinthopodium neuranthum	200100001300011120001001010000001100
Merinthopodium pendulum	20010100130001 0?2000?????01010100110
Schultesianthus uniflorus	211001010000010 0?0001?????01101100100
Schultesianthus venosus	21100101000001001000 1?????01101100100
Schultesianthus crosbianus	211001010010011000001000100110110 0100
Schultesianthus megalandrus	210001010001011000001001010110000000
Schultesianthus leucanthus	21000101000101100000100101011000000 0
Schultesianthus odoriferus	210001010001011000001?????01100000000
Schultesianthus coriaceus	210001010001011000001001010110000000 0
Schultesianthus dudleyi	21000101000101100000 1?????01100000000
Juanulloa pavonii	200011000000110110001100000100100000 1
Juanulloa wardiana	202011000120 00?111010101000101100000 1
Juanulloa globifera	20201100011000?111010????????????????
Juanulloa speciosa	201001000120010110001000000000000 1110
Juanulloa ochracea	200001000100010110000000000000000 1110
Juanulloa parasitica	200101000120010110000000010010010000 1
Juanulloa ferruginea	200101000120010100000000100100000000
Juanulloa membranacea	200100000120010110 00?????01001000101
Juanulloa verrucosa	200100000100010110 00?0001001000101
Juanulloa parviflora	200101000100010110 00????????????????
Juanulloa mexicana	200001000120010110000000010010000001
Dyssochroma longipes	201011101300010010 00?????00000100100
Dyssochroma viridiflora	201011101300010020 00?????00000100100
Trianaea speciosa	200111001300011220001000000000 1100100
Trianaea brevipes	201011000000011220001000000010010001 10
Trianaea neovisae	200011001300011220001????????????????
Trianaea nobilis	200111001300011220001000000000 1000110
Trianaea naeka	201111001300010220 00?????00000000100
Trianaea sp4	201011000?000????000????????????????

Persson et al. (1994). Minute, peltate, glandular trichomes (character 1) on the leaves of *Schultesianthus* were first described by Bernardello and Hunziker (1991) and are either present or absent on both leaf surfaces. These trichomes are sunken into small pits in the mesophyll so that the ca. 24 cell head is at about the same level as the foliar surface. The trichomes appear as minute reddish dots to the naked eye and are usually, but not always, more abundant on the abaxial leaf surface. Corolla aes-

→

Figure 4. One of the two equally parsimonious cladograms from the Hennig86 analysis. The tree shown here is identical to that produced by NONA, and to the consensus tree. The characters are discussed in the text, and character states are shown in Table 2. For characters marked on the branches of the cladogram: stippled marks indicate reversals and parallelisms (homoplasy) and solid marks non-homoplastic synapomorphies.


Nicandra
Atropa
Lycium
Juanulloa verrucosa
Juanulloa membranacea
Juanulloa parasitica
Juanulloa ferruginea
Juanulloa mexicana
Juanulloa pavonii
Juanulloa wardiana
Juanulloa globifera
Markea lopezii
Markea aff lopezii
Solandra brachycalyx
Solandra boliviana
Schultesianthus venosus
Schultesianthus uniflorus
Schultesianthus crosbianus
Schultesianthus megalandrus
Schultesianthus leucanthus
Schultesianthus odoriferus
Schultesianthus coriaceus
Schultesianthus dudleyi
Markea panamensis
Markea ulei
Markea sessiliflora
Markea costanensis
Markea coccinea
Markea formicarum
Markea camponoti
Juanulloa speciosa
Juanulloa ochracea
Juanulloa parviflora
Merinthopodium pendulum
Merinthopodium neuranthum
Trianaea naeka
Dyssochroma longipes
Dyssochroma viridiflora
Trianaea speciosa
Trianaea nobilis
Trianaea neovisae
Trianaea brevipes
Trianaea sp.nov.

tivation (character 8) has been coded as either overlapping or valvate. The exact arrangement of overlapping corolla lobes in bud is sometimes difficult to determine from herbarium specimens and occasionally varies in a species or genus. Corolla ontogeny has not shed any light on the relative plesiomorphy or apomorphy of such differing aestivation patterns in the Acanthaceae (Scotland et al., 1994). Thus, should this character be used in subsequent analyses of the Juanulloeae, it should be unordered and unweighted.

Results and Discussion

In the analysis of the genera of the Juanulloeae, two trees of length = 129, CI = 35, and RI = 71 were found by Hennig86 (see Fig. 4), and one of these two trees was also found by NONA. If only *Nicandra* is used as the outgroup, Hennig86 finds three trees, again of length 129, one of which is identical to the strict consensus tree. The two trees found by Hennig86 using all three outgroup taxa differ only in the resolution of *Schultesianthus*, with tree 2 being over-resolved owing to character state assignment from missing data. Tree 1 is identical to that found by NONA, which does not attempt to resolve nodes with missing data. In the NONA analysis, 15 of 50 replications were of length 129, indicating this is probably the shortest tree.

Using successive approximation weighting in Hennig86 character weights stabilized after four iterations, giving 444 trees of L = 280, CI = 67, and RI = 88. Reading all 444 trees back onto the unweighted data set gave trees of length 135 or 136, which is longer than the most parsimonious trees by 6 or 7 steps. Using the alternative weighting system of Goloboff (1993) we obtained one tree of length = 130 (not shown), one step longer than our most parsimonious tree generated using unweighted data. This tree differs in the positions of the three anomalous species of *Juanulloa* (see below) and in the order of branching in the *Trianaea* clade.

The stabilized weights from the successive approximation weighting analysis are presented in Table 4. Weights of 10 imply perfect fit to the tree, while weights of 0 (and lower numbers in the PeeWee analysis) imply the character is of poorer fit. Of the characters with weights of 10 in the Hennig86 analysis, two (character 12, presence of a filament tube, and character 26, presence on pollen of spiny supratectal processes) are uninformative (autapomorphic) and do not contribute to group formation on the tree. Only nine other characters had weights of 10, while the rest had low weights of 5 to 0, indicating the data set has a great deal of homoplasy and very low support. Of the characters traditionally used to define genera in the Juanulloeae (see Hunziker, 1977, 1979), corolla aestivation (character 8 in our analysis) and floral symmetry (character 7) perform better, while other characters, such as the insertion of the filament on the anther (character 15), are less consistent on our tree. Micromorphological characters such as the minute glandular trichomes characteristic of *Schultesianthus* (character 1, see below), the relative thicknesses of sexine and nexine layers in pollen

Table 4. Stabilized character weights from Hennig86 successive approximation analysis and weights (character fit) from PeeWee analysis (see text for explanation).

Character number	Character weight Hennig86	Character weight PeeWee
0	10	10
1	10	10
2	3	4.2
3	0	4.2
4	1	4.2
5	0	4.2
6	5	7.5
7	10	10
8	10	10
9	5	4.2
10	0	2.5
11	2	6
12	10	
13	1	5
14	2	5
15	2	4.2
16	1	3
17	3	7.5
18	10	10
19	10	10
20	1	5
21	4	7.5
22	10	10
23	1	6
24	2	5
25	3	7.5
26	10	
27	1	5
28	4	7.5
29	1	6
30	0	3.3
31	0	3.3
32	10	10
33	2	7.5
34	1	5
35	0	6
36	10	10

(character 36), and some pollen aperture characters (character 32) are a good fit to the tree and are useful in resolving relationships in this group.

Four main clades are identified in the Juanulloeae. The tribe is defined relative to the outgroups by its epiphytic habit (character 0), and the presence of anthers included in the mouth of the corolla tube (character 16, reversed several times in the group). The first clade, comprising species of *Juanulloa*, is sister group to the rest of the tribe (see Fig. 4). The members of this clade share synapomorphies in characters 3 (elongate inflorescence—reversed in *J. wardiana, J. globifera, J. pavonii,* and *J. mexicana*), 9 (narrow tubular flowers), and 36 (pollen with the nexine thicker than the sexine). *Juanulloa pavonii* + (*J. wardiana* + *J. globifera*) share a large suite of characters, many of which are shared with other taxa in the tribe (i.e., homoplasious): these include calyx lobes equal in length to the corolla tube (character 4) and pale brown, reniform seeds (characters 21 and 24). *Juanulloa wardiana* and *J. globifera* have been segregated as the genus *Rahowardiana* (D'Arcy, 1973 [1974]; Knapp & D'Arcy, 1993), but the results of this analysis indicate their relationships lie with *Juanulloa*, and perhaps they are deserving of subgeneric recognition. Three species of *Juanulloa* are in an anomalous position on the tree: *J. speciosa, J. ochracea,* and *J. parviflora. Juanulloa parviflora* is known only from the type, which bears a single flower, and thus many of the characters used in this analysis had to be scored as missing. Missing data can affect placement of taxa and resolution of trees and should therefore be viewed with caution (Platnick et al., 1991). *Juanulloa speciosa* and *J. ochracea* share a distinctive pollen type (see Persson et al., 1994) and pollen characters contribute largely to their position in the *Trianaea* (see below) clade. We do not have confidence in this placement, and thus have elected to keep these three species in *Juanulloa* pending further investigation. *Juanulloa speciosa* was originally described as the genus *Sarcophysa* by Miers (1857), and is morphologically somewhat isolated in the genus. The relationship of these taxa to the rest of *Juanulloa* is a subject that would bear investigation using molecular techniques.

The second main clade consists of *Markea lopezii* and a related, undescribed taxon, the species of *Solandra* treated in this analysis and the genus *Schultesianthus.* This clade is united by the possession of solitary flowers (character 2, reversed in part of *Schultesianthus*) and basifixed anthers (character 15, in parallel with several other taxa in the tribe). *Markea lopezii* and its undescribed relative are both known only from flowering specimens, and thus the matrix has many missing entries. *Markea lopezii* has anomalous pollen in the group, with prominent spiny supratectal processes (Persson et al., 1994), and its relationships need to be investigated further. Not all species of *Solandra* were included in this analysis, but these results indicate that it along with *M. lopezii* and *M.* aff. *lopezii* are the sister group to *Schultesianthus* and thus should be included in the tribe. However, cpDNA results (Olmstead et al., in press), using only four taxa of the group (*Solandra, Markea, Dyssochroma,* and *Juanulloa*), indicate that *Solandra* is the sister group of the rest of the Juanulloeae. Since no species of *Schultesianthus* were sampled in the cpDNA studies, this potential conflict remains to be solved. Many of the species of *Schultesianthus* were first described as *Solandra* (see Conspectus) owing to their close morphological similarity, and the species now recognized as *Schultesianthus* were thought to be intermediate between *Markea* and *Solandra* by D'Arcy (1973 [1974]).

All the species of *Schultesianthus* share a number of synapomorphies, two of which (character 1, peltate glandular trichomes and character 7, zygomorphic flowers) are found nowhere else on the tree. The genus also has two pollen synapomorphies: character 28, copious Ubisch bodies, and character 31, a discontinuous tectum (Persson et al., 1994). *Schultesianthus venosus, S. uniflorus,* and *S. crosbianus* differ from the rest of the genus as traditionally defined (see Bernardello & Hunziker, 1991) in their flowers with non-declinate stamens and style, but share all other synapomorphies of the group (see also Conspectus and D'Arcy, 1973 [1974]). These species are known from very few collections.

The genus *Markea* comprises the third main clade, united by the possession of pale tan (character 24) and rectangular seeds (character 21) with elongate testal cells (character 22) (see Fig. 4). The species *M. panamensis* and *M. ulei* have been separated as the genus *Hawkesiophyton* (Hunziker, 1977) and are probably worthy of subgeneric status. A species not treated in this analysis (it is known only from the type, which consists of a single poorly preserved flower), *M. sturmii* Cuatr., is superficially similar to *M. ulei* and should be examined more closely. The peculiar seed type seen in *Markea* is perhaps related to ant dispersal, as most of the species in this group are associated with ants in various ways (see above and Ducke, 1915). Many ant-dispersed seeds bear large elaiosomes (oil or fat bodies) that make them attractive to ants (see references in Willson, 1983). This is apparently not

Figure 5. SEM of seeds of *Markea coccinea* Rich. (Brazil, *Krukoff 6531*, BM).—A. Whole seed, scale bar = 278µm.—B. Close-up of tectal surface, scale bar = 34.5 µm.

the case in *Markea* (see Fig. 5), but fresh material must be examined to determine this for certain. In the genus *Datura*, the elaiosome often drops off when plants are dried and mounted on herbarium sheets (see Persson et al., in press). The seeds of *Markea* seem to have a fine reticulum of sticky threads on top of the testa (see Fig. 5B), which may make them stick to ants, thus causing them to be deposited in ant gardens.

The fourth clade in the tribe is that containing the genera *Merinthopodium*, *Dyssochroma*, and *Trianaea*. Three species of *Juanulloa* are also present in this clade, but as discussed above, are probably not correctly placed here. The clade (minus the species of *Juanulloa*) is united by synapomorphies in characters 8 (valvate aestivation, reversed in some species of *Trianaea*), 9 (campanulate flowers), and 16 (filaments exserted from the corolla tube). In general members of this clade all possess large, campanulate, greenish or greenish purple flowers (see Fig. 3) that are pollinated by bats (Vogel, 1958; Cuatrecasas, 1959; Baker, 1973; Voss et al., 1980). Voss et al. (1980), studying *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. at Finca La Selva, Costa Rica, postulated that it was adapted for pollination by traplining bats, as the flowers fell early in the night, were borne singly, and were odorless. Like many of the other species of the Juanulloeae these plants are only rarely collected, but in addition to this, each sheet often consists only of a single flower, making dissection undesirable and incompatible with the preservation of the specimen (this has also been noted as a problem in the study of *Solandra*; see Bernardello & Hunziker, 1987). The distinctive filament base morphology mentioned in the generic description is not visible in pressed specimens, but is likely to occur in all species of *Trianaea*. Ovary structure, a character that would separate *Trianaea* (with a 4–5-carpellate, 8–10-loculate ovary) from *Merinthopodium* and *Dyssochroma* (with bicarpellate, 4-loculate ovaries), can only rarely be assessed even with fruiting specimens.

We showed (Persson et al., 1994) that the twelve pollen types in the tribe did not cut across the boundaries of the main clades. However, although they serve effectively for the purposes of identification, palynological characters alone provided little resolution of relationships among the taxa. The inclusion of palynological characters in the present analysis increases the number of character states that can be sampled from the relatively few specimens that are available for many of the species. It contributes to the resolution of relationships and may also serve to identify functionally correlated syndromes of characters, such as those found in bat-pollinated species.

This analysis clearly highlights some of the problems with the characters used to identify and recognize the genera of the Juanulloeae. As previously defined, the genera were not monophyletic although many of the characters used in their definition are phylogenetically informative. The relationships of the monophyletic groups we have recognized in this study have not been fully resolved. The weak support for the basal clades in our tree indicates that more work is needed at this level within the tribe. Many of the genera have never been adequately monographed, and field-based studies will prove essential for the ultimate resolution of phylogenetic relationships in the group as additional characters that may prove useful are likely to be found in living plants. The extension of molecular systematics to a more comprehensive sample of the species may

also help to resolve many of the remaining uncertainties.

Conspectus of the Juanulloeae (including *Solandra*)

This generic conspectus is designed to allow the reader to identify herbarium specimens and, to some extent, living plants. For each genus a description, a list of the species, and references to published monographs or illustrations are provided. The species not included in the cladistic analysis are indicated with asterisks. Synonyms are listed after each accepted name. Directions for further investigation and work in progress are discussed for each genus.

1a. Corolla limb broadly campanulate, greenish or yellow, more than 5 cm long.
  2a. Corolla yellow sometimes with purplish streaks in the throat (bluish in *S. boliviana*), usually greater than 13 cm long, the stamens declinate; ovary somewhat inferior 6. *Solandra*
  2b. Corolla greenish or greenish purple, usually less than 13 cm long, the stamens regular; ovary completely superior.
    3a. Corolla vernation imbricate (occasionally valvate); anthers ventrifixed; filaments conspicuously geniculate at the base, covering the nectary; ovary 8–10-locular ..... 7. *Trianaea*
    3b. Corolla vernation valvate; anthers either basifixed or dorsifixed; filaments not conspicuously geniculate; ovary biocular.
      4a. Anthers basifixed; inflorescences consisting of a single flower; SE Brazil in Atlantic forest ..... 1. *Dyssochroma*
      4b. Anthers dorsifixed; inflorescences of 1–many flowers, with long and flexible axes; Central and N South America ..... 4. *Merinthopodium*

1b. Corolla limb tubular to narrowly campanulate, not broadly campanulate and bell-shaped, variously colored, cream to bright orange, usually less than 5 cm long.
  5a. Flowers zygomorphic, at least somewhat (difficult to see in pressed specimens of some species), cream fading yellowish, sweetly fragrant; calyx thick and coriaceous, drying somewhat woody; leaves with minute peltate glandular trichomes on both surfaces; stems pubescent in new growth 5. *Schultesianthus*
  5b. Flowers regular, orange, cream or greenish, not fragrant; calyx various, but not drying woody; leaves lacking minute peltate glandular trichomes; stems glabrous or pubescent.
    6a. Anthers basifixed; corolla funnelform or infundibuliform, usually yellowish or greenish (bright orange-red and nearly salverform in *M. coccinea*), the tube and lobes membranous in texture; fruit thin-walled, the seeds elongate, pale or orange ..... 3. *Markea*
    6b. Anthers dorsifixed; corolla narrowly tubular (in *J. paronii* the tube very short), white, orange or reddish, the tube and lobes thick and fleshy in texture; fruit not thin-walled as above, often somewhat woody, the seeds reniform, usually dark brown ..... 2. *Juanulloa*

Figure 6. *Dyssochroma viridiflora* (Sims) Miers (Sims, J. 1818. Curtis's Botanical Magazine 45: t. 1948).

1. Dyssochroma Miers, Ann. Mag. Nat. Hist. ser. 2, 4: 250. 1849. TYPE: *Dyssochroma viridiflora* (Sims) Miers (basionym: *Solandra viridiflora* Sims, 1818). Figure 6.

Epiphytic shrubs or small trees, occasionally terrestrial; stems pendulous, the bark thin, flexible and exfoliating, drying a dark, reddish brown. Leaves elliptic, 5–12 × 2.5–5 cm, coriaceous, glabrous. Inflorescence terminal, a highly modified cyme, congested, often consisting of a single flower,

glabrous. Buds elliptic, the corolla aestivation valvate. Pedicels glabrous. Flowers with the calyx divided nearly to the base, the lobes 3–4 cm long, triangular, acuminate at the tips, coriaceous, glabrous; corolla greenish or greenish purple, broadly flaring to campanulate, the tube 5–6 cm long, the lobes 1–2.5 cm long, at anthesis strongly reflexed; filaments adnate to the corolla tube in the lower ⅓, exserted or included, 7–9 cm long, glabrous along their whole length; anthers basifixed, 1–1.5 cm long; pollen 3-colporate with long colpi and uneven reticulate ornamentation; ovary superior, glabrous; style glabrous, 8–10 cm long, the stigma clavate. Fruit and seeds not known. 2 spp., SE Brazilian rainforests.

List of species. *Dyssochroma longipes* (Sendtn.) Miers, Brazil (*Markea longipes* (Sendtn.) Cuatr., *Solandra longipes* Sendtn.); *D. viridiflora* (Sims) Miers, Brazil (*Dyssochroma albidoflavum* Lemaire, *Markea peckoliorum* Gilg, *M. viridiflora* (Sims) Ducke, *Solandra viridiflora* Sims).

Dyssochroma may be congeneric with *Trianaea*, but since so few specimens of these plants are known and nothing is known about the fruits or seeds, we have maintained it as distinct pending further investigation. The pollen is identical to most species of *Trianaea* but differs from that of *T. speciosa* in that the reticulate ornamentation is discontinuous, so that areas close to the poles lack muri (see Persson et al., 1994).

The two described species of *Dyssochroma* are in fact only different stages of floral development (L. F. de Carvalho, pers. comm.), with the included anthers of *D. longipes* occurring at earlier stages of flowering, while the exserted anthers of *D. viridiflora* are often seen on flowers found on the forest floor post-flowering. Future studies being carried out at the Jardim Bôtanico de Rio de Janeiro will clarify this situation.

2. Juanulloa Ruiz & Pavón, Prodr. Fl. Peruv. 27, t. 4. 1794. TYPE: *Juanulloa parasitica* Ruiz & Pavón. Figures 2A, 7.

Ectozoma Miers, Ann. Mag. Nat. Hist. ser. 2, 3: 166. 1849. TYPE: *Ectozoma pavonii* Miers.

Laureria Schlechtendahl, Linnaea 8: 513. 1833. TYPE: *Laureria mexicana* Schltdl.

Portaea Tenore, Atti 7a. Adum. Sc. Ital. 902, t. 1846. TYPE: *Portaea aurantiaca* Tenore.

Rahowardiana D'Arcy, Ann. Missouri Bot. Gard. 60: 670. 1973 [publ. 1974]. TYPE: *Rahowardiana wardiana* D'Arcy.

Sarcophysa Miers, Ann. Mag. Hist. ser. 2, 4: 190. 1849. TYPE: *Sarcophysa speciosa* Miers.

Ulloa Pers., Syn. Pl. 1: 128. 1805. TYPE: *Juanulloa parasitica* Ruiz & Pavón.

Epiphytic shrubs or small trees, the stems often hanging and pendulous from the canopy, 1–20 m; bark of stems loose and exfoliating when dry, often reddish or reddish brown. Leaves elliptic, ovate or obovate, 6–30 × 5–9 cm, usually petiolate (sessile in *J. verrucosa*), membranous or coriaceous, glabrous or pubescent, the trichomes uniseriate, simple or more often branched. Inflorescence terminal or lateral, a variously modified cyme, occasionally somewhat raceme-like, often many times branched, the peduncle often very long and pendulous, usually many flowered (10–50) but occasionally reduced to 1–2 flowers (*J. speciosa*), glabrous or pubescent, the trichomes uniseriate, simple or branched, buds elongate, usually exserted from the calyx tube, corolla aestivation quincuncial or imbricate. Flowers with the calyx lobed nearly to the base or unlobed and inflated (*J. speciosa*), usually somewhat fleshy and bright colored, ½ to equal to the length of the corolla tube; corolla fleshy, funnelform to narrowly tubular, 1–9 cm long, red, orange, or cream with reddish or purple markings, the tube either flaring at the apex (*J. pavonii, J. ferruginea*) or more commonly slightly constricted, the lobes minute and rounded or equal in length to the tube (*J. pavonii, J. ferruginea*); filaments inserted near the base or ca. ½ way along the tube, densely pubescent with uniseriate trichomes at the point of insertion; anthers included in the corolla tube at anthesis, very variable in size, dorsifixed; pollen 3-colporate, either with long, narrow colpi and scabrate-rugulate ornamentation or with short, broad colpi and a scabrate-perforate ornamentation; ovary ovoid to conical or beaked (*J. wardiana, J. globifera*), glabrous; style glabrous, ± equal to the filaments, usually somewhat longer at anthesis, the stigma capitate to somewhat clavate, bilobed. Fruit green berry, ovoid to conical, usually within the accrescent calyx, 1–3 cm long (in *J. wardiana* and *J. globifera* seeds are borne in the ovary beak, but mature fruits are unknown); seeds reniform, quite large, 2–7 × 1.5–3 mm, dark brown or reddish brown. 11 spp., Mexico to Bolivia.

Literature. Hunziker & Subils (1991).

List of species. *Juanulloa ferruginea* Cuatr., Colombia to Peru; *J. globifera* (S. Knapp & D'Arcy) S. Knapp, NW Colombia (*Rahowardiana globifera* S. Knapp & D'Arcy); *J. membranacea* Rusby, Bolivia (*J. pedunculata* Rusby); *J. mexicana* (Schlechtendahl) Miers, Mexico and Central America to N Colombia (*J. aurantiaca* Otto & Dietr., *J. bicolor* Gleason, *J. elliptica* Dunal, *J. hookeriana* Miers, *J. panamensis* Miers, *J. sargii* Donn. Sm., *Laureria mexicana* Schlechtendahl, *Markea tomentosa* Lun-

Figure 7. *Juanulloa pavonii* (Miers) Benth. & Hook. as *Ectozoma Pavonni* (plate 48 from Miers, J. 1857. Illustrations of South American Plants).

dell, *Portaea aurantiaca* Tenore); *J. ochracea* Cuatr., Colombia to Peru; *J. parasitica* Ruiz & Pavón, Ecuador, Peru, and Brazil (*Ulloa parasitica* (Ruiz & Pavón) Pers.); *J. parviflora* (Ducke) Cuatr., Brazil, near Manaus (known only from the type) (*Markea parviflora* Ducke); *J. pavonii* (Miers) Benth. & Hook., W Ecuador and NW Peru (*Ectozoma pavonii* Miers, *Markea pavonii* (Miers) D'Arcy); *J. speciosa* (Miers) Dunal, Colombia and Ecuador (*Sarcophysa speciosa* Miers); *J. verrucosa* (Rusby) Hunz., Bolivia (*Markea verrucosa* Rusby); *J. wardiana* (D'Arcy) S. Knapp, Panama (*Rahowardiana wardiana* D'Arcy).

The flowers of most of the species of *Juanulloa* conform to the classic hummingbird pollination syndrome: they are tubular, brightly colored and very thick and fleshy (Fig. 2A). However, *J. pavonii* (Fig. 7) and *J. ferruginea* (and also perhaps to some extent *J. parviflora*) have quite different flowers, which are greenish, with shorter tubes and somewhat reflexed lobes. These perhaps represent a different pollination syndrome.

Figure 8. *Markea coccinea* Rich. (plate 45 from Miers, J. 1857. Illustrations of South American Plants).

The very condensed globular inflorescence of *Juanulloa wardiana* and *J. globifera* is unique in the tribe, and in the family Solanaceae (illustrations can be seen in Knapp & D'Arcy, 1993). In these species the calyx as well as the corolla is brightly colored and quite showy. These flowers are apparently visited by hummingbirds, and produce copious nectar.

There are two types of pollen found in this genus (Persson et al., 1994). In *Juanulloa speciosa* and *J. ochracea* the pollen is 3-colporate with long, narrow colpi and scabrate/rugulate exine ornamentation. In the rest of the genus the pollen is 3-colporate with short, broad colpi and a scabrate/perforate exine ornamentation.

3. Markea Rich., Actes Soc. Nat. Hist. Paris 1: 107. 1792. TYPE: *Markea coccinea* Rich. Figure 8.

Hawkesiophyton Hunz., Kurtziana 10: 39. 1979. TYPE: *Hawkesiophyton panamense* (Standl.) Hunz. (basionym *Markea panamensis* Standl.).

Lamarkea Pers., Synopsis 1: 218. 1805. TYPE: *Lamarkea*

coccinea (Rich.) Pers. (basionym *Markea coccinea* Rich.).

Epiphytic shrubs or small trees, occasionally growing on the forest floor in cloud forest. Leaves elliptic to ovate, 5–25(–40) × 2.5–10(–20) cm, coriaceous or membranous, glabrous or pubescent, the trichomes simple and uniseriate, multicellular. Inflorescence a variously modified cyme, sometimes superficially raceme-like, branched or simple, glabrous to minutely pubescent, ± sessile (*M. sessiliflora*), to borne on an elongate peduncle (*M. coccinea*), 1–25 cm long, bearing 1–10 flowers at a time, but with many scars, data on specimen labels indicating that only one flower opens at a time. Buds elongate, corolla aestivation imbricate or cochlear. Pedicels glabrous or pubescent. Flowers with the calyx lobed nearly to the base, the lobes long-triangular, 0.8–3 cm long, often with distinctively colored venation and long-acuminate tips, glabrous or pubescent; corolla bright orange (*M. coccinea*) or more often greenish purple or cream colored, salverform (*M. coccinea*) to funnelform, the tube 1–7 cm long, the lobes 0.5–1.2 cm long, rounded and the margins occasionally somewhat laciniate, not reflexed at anthesis, glabrous or pubescent with simple, uniseriate trichomes on the exterior surfaces; filaments adnate to and included in the corolla tube, ± equal in length to the corolla tube or ca. ½ its length, pubescent at the point of insertion; anthers basifixed, elongate, ca. 2 mm (*M. ulei, M. panamensis*) to ca. 1 cm (*M. sessiliflora, M. camponoti*) long, longitudinally dehiscent; pollen 3-colporate, ornamentation and apertures varying; ovary superior, glabrous; style usually equal in length with the filaments, or longer and held at the mouth of the corolla tube, the stigma clavate. Fruit an ellipsoid berry, 1–2 × ca. 1 cm, green when ripe, the apex somewhat beaked from the persistent style base, the pericarp thin and papery when dry, in herbarium specimens often almost translucent, held within the accrescent calyx; seeds many, long rectangular, 2–5 × ca. 0.5 mm, usually bright orange. 9 spp., Panama to S Peru.

List of species. *Markea camponoti* Ducke, upper Amazon basin; *M. coccinea* Rich., upper Amazon basin to the Guianas (*Lamarckea coccinea* Pers.); *M. costanensis* Steyerm., Venezuela, Cordillera de la Costa; *M. formicarum* Dammer, Amazon basin, on white sand; *M. longiflora* Miers, Trinidad (this may in fact be an older name for the taxon herein referred to as *M. camponoti*, but the species has not been recollected in Trinidad since the type specimen, which has a single, badly damaged flower); *M. panamensis* Standl., Panama and adjacent Colombia (*Hawkesiophyton panamense* (Standl.) Hunz., *M. dimorpha* C. V. Morton); *M. sessiliflora* Ducke, N Amazon basin, Guianas, Roraima plateau (*M. porphyrobaphes* Sandwith, *M. reticulata* Steyerm. & Macguire); **M. sturmii* Cuatr., Colombia; *M. ulei* (Dammer) Cuatr., upper Amazon basin (*Ectozoma ulei* Dammer, *Hawkesiophyton klugii* Hunz., *H. ulei* (Dammer) Hunz.).

Markea as here defined is composed of two main clades, one consisting of the small greenish-flowered taxa previously treated as the genus *Hawkesiophyton*, *M. ulei* and *M. panamense*, which perhaps deserve sectional or subgeneric rank. *Markea sturmii*, not treated in the cladistic analysis, is somewhat intermediate between the small-flowered clade and the following. The other clade consists of five taxa, again divided into two clear groups: one with short inflorescences and flowers drying dark on the herbarium sheet (*M. sessiliflora, M. costanensis*) and the other consisting of mainly Amazonian species with long-acuminate calyx lobes with distinctive venation and usually elongate inflorescences.

The three types of pollen found in this genus (Persson et al., 1994) correlate closely with these groups. All are 3-colporate but they differ in exine sculpturing and aperture type. In *M. ulei* and *M. panamensis* the colpi are long and narrow and the apertures distinctly beaked. Short colpi occur in the *M. camponoti* type, where the ornamentation is baculate and in the *M. sessiliflora* type, where it is microreticulate to scabrate.

The genus *Markea* is in dire need of a field-based monograph.

4. Merinthopodium Donn. Sm., Bot. Gaz. 23: 11. 1897. TYPE: *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. (basionym: *Markea neurantha* Hemsl.). Figures 3A, 9.

Epiphytic shrubs or small trees, 1–10 m, often clambering over branches and hanging from the canopy; bark loose and exfoliating, bright silvery-gray. Leaves elliptic to obovate, occasionally strongly three-veined from the base, 10–15 × 5–9 cm, glabrous to minutely puberulent along the main veins beneath, the trichomes simple and uniseriate. Inflorescence an elongate, pendulous raceme, the peduncle 15–50 cm long, minutely pubescent with tuberculate trichomes with multiseriate bases bearing one or two uniseriate simple branches, the branches breaking off leaving the tuberculate bases which cause a warty roughened texture on the peduncle, flowers borne only at the tip or distal ¼, usually only 2–7 at a

Figure 9. *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. (plate from Donnell Smith, J. 1897. Bot. Gaz. (Crawfordsville) 23).

time, but the inflorescence with up to 100 scars. Buds ellipsoid, rapidly elongating to exceed the calyx tube, corolla aestivation valvate. Flowers with the calyx usually ¼ the length of the corolla tube at anthesis, membranous to coriaceous, lobed nearly to the base, the lobes with blunt tips; corolla greenish to greenish with various purple markings, the tube 3–10 cm long, flaring early in anthesis but at full anthesis broadly campanulate, the lobes ca. 2 cm long, strongly reflexed at anthesis; filaments adnate to the base of the corolla tube, exserted from it at anthesis, glabrous; anthers bright yellow, dorsifixed and somewhat versatile; pollen generally large, 3-colporate with scabrate ornamentation and protruding apertures; ovary bilocular, glabrous; style glabrous, ± equal to the length of the filaments at anthesis, the stigma capitate, bright green, strongly bi-lobed. Fruit a green berry, ovoid, 1–2.5 cm long, the pericarp ± membranous, not leathery or woody; seeds many, 1.5–2 × 0.5–1 mm, reniform, reddish brown. 3 spp., S Mexico to N Venezuela and Colombia.

List of species. Merinthopodium neuranthum

(Hemsl.) Donn. Sm., S Mexico and Central America (*Markea campanulata* (Donn. Smith) Lundell, *Markea gentlei* Lundell, *Markea internexa* (Blake) Lundell, *Markea leptesthema* (Blake) Cuatr., *Markea neurantha* Hemsl., *Me. campanulatum* Donn. Smith, *Me. internexum* Blake, *Me. leptesthemum* Blake); *Me. pendulum* (Cuatr.) Hunz., Colombia and Venezuela (*Markea pendula* Cuatr.); **Me. vogelii* (Cuatr.) Castillo & R. E. Schultes, Colombia and Venezuela (*Markea vogelii* Cuatr.).

The shape of the flowers of *Merinthopodium* depends greatly on their state when collected. These plants bloom at night and are probably pollinated by bats (see Voss et al., 1980). Thus flowers collected before full anthesis are shaped like a flaring tube, but when fully in bloom, the limb becomes broadly campanulate with strongly reflexed lobes. This same situation occurs in *Trianaea* and *Dyssochroma*. The peculiar trichomes found on the peduncle of *Merinthopodium* are also found in *T. naeka* S. Knapp of eastern Ecuador. One of the reasons why there are many synonyms in this genus is that specimens collected at different stages of flowering have been regarded as distinct species. There is also geographical variation in flower size and leaf texture.

5. Schultesianthus Hunz., Kurtziana 10: 35. 1977. TYPE: *Schultesianthus leucanthus* (Donn. Sm.) Hunz. (basionym: *Markea leucantha* Donn. Sm.). Figure 10.

Epiphytic shrubs or small trees, occasionally terrestrial in wet cloud forests; bark usually somewhat reddish, glabrous or pubescent with simple uniseriate trichomes on the new growth; leaves borne in congested groups separated by long naked internodes. Leaves elliptic, 6–15 × 2.5–9 cm, thick and coriaceous, drying pale green or brownish, often rounded at the tip, glabrous or pubescent with simple uniseriate trichomes, in addition all species bearing minute glandular trichomes each with a unicellular base and multicellular head sunk in a pit on the upper and lower surfaces, giving the appearance of small red dots on dry specimens. Inflorescence a terminal cyme, variously branched, occasionally reduced to a single flower (*Sch. crosbianus*), glabrous or variously pubescent with simple uniseriate trichomes. Buds elongate, the apex swollen, corolla aestivation quincuncial or cochlear. Pedicels glabrous or pubescent, usually quite short. Flowers with the calyx very coriaceous, lobed ½ way or nearly to the base, the lobes strongly overlapping, glabrous or minutely glandular pubescent, becoming woody and accrescent in fruit; corolla funnelform to strongly infundibuliform, 4–15 cm long, occasionally somewhat zygomorphic, strongly and sweetly fragrant, pale green to cream (black in *S. crosbianus*), yellowing with age, the lobes rounded and often somewhat laciniate; filaments adnate with the corolla tube in the lower ⅓, densely pubescent at point of insertion and ca. ½ way to the anthers above, regular or declinate, exserted from the corolla tube at anthesis; anthers small and elliptic, or slightly larger and more elongate (in *Sch. venosus, Sch. uniflorus,* and *Sch. crosbianus* with non-declinate filaments); pollen 3-colporate, rugulate and covered in Ubisch bodies; ovary glabrous, somewhat pointed, bilocular; style declinate or straight, glabrous, the stigma broadly capitate, distinctly 2-lobed. Fruit a green to purplish green berry, 1–3 cm long, ovoid or somewhat pointed, woody when dry, very leathery and fleshy when fresh, invested in the accrescent woody calyx; seeds many, reniform, large, 5–6 × 3–4 mm, pale yellowish tan or dark brown. 8 spp., Mexico to Bolivia.

Literature. Bernardello & Hunziker (1991).

List of species. Schultesianthus coriaceus (Kuntze) Hunz., Antioquia, Colombia (*Solandra coriacea* Kuntze); *Sch. crosbianus* (D'Arcy) S. Knapp, Costa Rica and Panama (*Markea crosbiana* D'Arcy); *Sch. dudleyi* Bernardello & Hunz., S Ecuador, S Peru; *Sch. leucanthus* (Donn. Sm.) Hunz., S Mexico to S Peru (*Markea leucantha* Donn. Sm., *Merinthopodium leucanthum* (Donn. Sm.) Blake, *Metternichia werklei* Schumann ex Bois); *Sch. megalandrus* (Dunal) Hunz., N Colombia and N Venezuela (*Markea megalandra* (Dunal) D'Arcy, *M. suaveolens* Standl., *Metternichia ? megalandra* Dunal, *Sch. suaveolens* (Standl.) Hunz., *Solandra megalandra* (Dunal) Killip & Pittier); *Sch. odoriferus* (Cuatr.) Hunz., Cordillera Oriental, Colombia (*Solandra odorifera* Cuatr.); *Sch. uniflorus* (Lundell) S. Knapp, Chiapas, Mexico (*Markea uniflora* Lundell, *Merinthopodium uniflorum* (Lundell) Hunz.); *Sch. venosus* (Standl. & C. V. Morton) S. Knapp, Costa Rica and Panama (*Markea venosa* Standl. & C. V. Morton).

D'Arcy (1973 [1974]), in his treatment of *Markea* for Flora of Panama, clearly and correctly identified the close relationships between the species of the present genus *Schultesianthus*. He recognized the three radially symmetrical flowered species, *Sch. crosbianus, Sch. uniflorus,* and *Sch. venosus,* as members of the "perhaps generically distinct" group including *Sch. leucanthus* (as *Markea megalandra* in his treatment).

Many of the species of *Schultesianthus* were originally described as *Solandra,* and *S. boliviana* and *Sch. coriaceus* have been considered "linking" spe-

Figure 10. *Schultesianthus leucanthus* (Donn. Sm.) Hunz. (*Hampshire & Whitefoord 469*, BM).

cies. For discussion see comments with the generic description of *Solandra*.

The flowers of *Schultesianthus* are among the most showy in the Juanulloeae (see Fig. 10). They are sweetly fragrant and change color from white to a creamy yellow with age. Large bees have been observed visiting the flowers, but little is known about their biology.

6. Solandra Swartz, nom. cons., Kongl. Vetensk. Acad. Nya Handl. 8: 300–306. 1787. TYPE: *Solandra grandiflora* Swartz. Figures 2B, 11.

Swartsia Gmelin, Systema naturae 2: 296, 390. 1791.
Solandera Kuntze, Rev. Gen. Plantarum. 452. 1891 (orthographic variant).

Woody lianas or high climbing epiphytic shrubs

Figure 11. *Solandra grandiflora* (Sims, J. 1817. Curtis's Botanical Magazine 44: t. 1874).

or small trees; stems glabrous or minutely pubescent, the trichomes glandular, simple or branched; bark shiny and loose, exfoliating when dry. Leaves elliptic, ovate or obovate, large and coriaceous, glabrous or pubescent with trichomes like those of the stems. Inflorescence terminal, a highly reduced cyme, usually with a single flower. Buds elongate, strongly exserted from the calyx tube, corolla aestivation quincuncial or cochlear. Pedicels at anthesis stout and woody. Flowers with the calyx 3–10 cm long, tubular, usually irregularly 2- to 5-lobed and zygomorphic, the lobes equal in length to the tube, occasionally somewhat purplish, glabrous or pubescent; corolla very large and showy, 13–40 cm long, zygomorphic, infundibuliform to cyathiform, white to cream or yellow, often with longitudinal purplish markings in the throat, darkening with age, the lobes rounded, entire to laciniate or fimbriate; filaments adnate to the corolla tube, exserted or included, declinate, densely pubescent at the point of insertion with simple, uniseriate trichomes; anthers basifixed, 6–13 mm long, longitudinally dehiscent; pollen 3-colporate, coarsely reticulate; ovary 2-carpellate, 4-locular, glabrous, partially sunken into the receptacle and thus partly inferior; style equal in length to the filaments, glabrous, declinate, the stigma minute and capitate, bilobed. Fruit a leathery berry, conical, green or yellow when ripe, the calyx persistent and accrescent but splitting in fruit; seeds round or reniform, 4–6 × 2.5–4 mm, the cotyledons incumbent (fide Bernardello & Hunziker, 1987). 10 spp., West Indies, Mexico to the Amazon basin.

Literature. Bernardello & Hunziker (1987).

List of species. Solandra brachycalyx Kuntze, Costa Rica and Panama; **S. brevicalyx* Standl., NE Mexico; *S. boliviana* Britton, Bolivia; **S. grandiflora* Swartz, West Indies, Central and South America (*Datura sarmentosa* Lam., *D. scandens* Vellozo, *S. hirsuta* Dunal, *S. nitida* Zucc., *S. minor* Griseb., *S. scandens* (Vell.) Toledo, *Swartzia grandiflora* (Swartz) Gmelin); **S. guerrerensis* Martínez, Duran-

go, Mexico; **S. guttata* D. Don, Mexico; **S. longiflora* Tussac, West Indies, N South America (*S. laevis* Hooker, *S. macrantha* Dunal, *S. grandiflora* var. *macrantha* (Dunal) Voss); **S. maxima* (Sessé & Moçiño) P. S. Green, Mexico, Central and N South America (*Datura maxima* Sessé & Moçiño, *S. hartwegii* N. E. Brown, *S. selerae* Dammer); **S. nizandensis* Matuda, Mexico, Guatemala, Honduras; **S. paraensis* Ducke, Amazon basin in Colombia, French Guiana, Brazil.

The species of *Solandra* are widely cultivated for their showy flowers (Fig. 2B) in the tropics and subtropics throughout the world. These large yellowish flowers open in the evening, possibly suggesting bat pollination. Species in the genus are used by the Huichol and other groups in Mexico as hallucinogens (see references in Bernardello & Hunziker, 1987). The partially inferior ovary of *Solandra* is unique in Solanaceae. It is deeply sunk into the receptacle at anthesis, but specimens in fruit appear to be totally superior.

Solandra boliviana has often been considered to be a "linking" species between *Solandra* and *Schultesianthus* as it is superficially similar to the large-flowered *Sch. coriaceus*. Our results, however, demonstrate that *S. boliviana* shares not only gross morphological but also pollen synapomorphies with the rest of *Solandra* but not *Schultesianthus* (see Persson et al., 1994). The two genera are closely related (in our analysis sister groups, but in the analysis of Olmstead et al., in press, somewhat separate, see beginning of this article).

7. Trianaea Planch. & Linden, Prix-Courant 8: 4. 1853. TYPE: *Trianaea nobilis* Planch. & Linden. Figures 3B, 12.

Poortmannia Drake, Bull. Soc. Philom. Paris, ser. 8, 4: 128. 1892. TYPE: *Poortmannia speciosa* Drake.

Epiphytic or terrestrial shrubs or small trees, often clambering over other vegetation; stems flexuous, often dark purple when young; bark smooth or verrucose, glabrous to densely pubescent, gray or reddish brown. Leaves usually very large, 10–30 × 1–10 cm, narrowly linear to broadly elliptic, shiny and coriaceous, glabrous to minutely pubescent, densely hirsute in *T. naeka*, the trichomes simple and uniseriate. Buds elliptic, ± halfway exserted from the calyx tube, corolla aestivation quincuncial or cochlear. Pedicels at anthesis short and stout to long (ca. 5 cm) and pendant. Flowers with the calyx usually ± equal to the corolla tube at anthesis, somewhat inflated and strongly 5-angled, lobed ca. ½ way to the base, coriaceous, usually drying dark reddish brown or black, often somewhat purplish in

Figure 12. *Trianaea speciosa* (Drake) Soler. (*Knapp et al. 9121*, Loja–Zamora road, Ecuador), scale bar = 2 cm.

live plants, glabrous to minutely pubescent with simple uniseriate trichomes; corolla very large and fleshy, 5–15 cm long, broadly campanulate, green or greenish with purplish red markings on the throat, glabrous or densely pubescent without, the trichomes simple and uniseriate, the lobes triangular in outline, strongly reflexed at anthesis, the margins revolute; filaments adnate to the corolla tube in the lower ¼, usually strongly geniculate at the base, connivent around the straight style, glabrous along their entire length; anthers elongate, 1–1.5 cm long, usually white, ventrifixed, somewhat versatile; pollen 3-colporate, reticulate, with long, narrow colpi; ovary glabrous or minutely pubescent, style straight, glabrous, the stigma large, capitate to clavate. Fruit a berry, 3–6 cm long, 8–10-locular, green or purplish, the pericarp leathery, the pulp fleshy; seeds very small, 1–2 × 0.5–1 mm, reniform, but very thin, pale yellowish tan. About 6 spp., Colombia to N Peru.

List of species. Trianaea brevipes (Cuatr.) S. Knapp, Colombia and Ecuador (*T. spectabilis* Cuatr. var. *brevipes* Cuatr.); *T. naeka* S. Knapp, SE Ecuador, Cordillera del Condor; *T. neovisae* Romero-Cas-

tañeda, Sierra Nevada de Santa Marta, Colombia; *T. nobilis* Planch. & Linden, Colombia and Ecuador; *T. speciosa* (Drake) Soler., S Colombia to N Peru (*Poortmannia speciosa* Drake, *T. spectabilis* Cuatr.); *T.* sp. nov., NC Peru, Cajamarca.

Trianaea is one of the most poorly collected genera in the Solanaceae. Its green flowers and position high in the canopy make it difficult to see and to access. The flowers of *Trianaea* are, like *Merinthopodium* and *Dyssochroma*, typical bat-pollinated flowers, and Vogel (1958) observed bats visiting the flowers of *T. brevipes* in Colombia. Persson et al. (1994) recognized two pollen types in the genus. However, although these show differences in the reticulum that enable them to be distinguished, they are very similar in overall pollen morphology.

The ovary of *Trianaea* is peculiar in Solanaceae in being 4–5-carpellate rather than the more typical 2-carpellate ovary found in the rest of the family (see Solereder, 1898, for a discussion). This character is difficult to see in flowering material, and as most specimens have a single flower, dissection is not desirable. Preserved collections are essential for the future study of this genus and its relationships to the rest of the green-flowered clade to which it belongs.

TAXA INCERTAE SEDIS

Markea lopezii Hunz., Cordillera Occidental, Colombia.—In the cladistic analysis this and a related species recognized but not named by Hunziker (1985) are the sister group of *Solandra*. The paucity of specimens for analysis and the fact that no fruiting specimens of *Markea lopezii* are known means this relationship needs further research. The pollen of *M. lopezii* is anomalous in the Juanulloeae (see Persson et al., 1994, and discussion above).

Several recent collections of epiphytic Solanaceae from Ecuador and adjacent Peru may certainly represent new taxa, and as more intensive collecting is done more specimens are likely to come to light.

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Appendix. Selected Specimens Examined.

Atropa belladonna L.—Morocco: *Mohamed 146* (BM).

Lycium cestroides Schltdl.—Bolivia: *Fiebrig 2213* (BM).

Nicandra physaloides (L.) Gaertner—Cultivated: *Higgins 149* (BM).

Dyssochroma longipes (Sendtner) Miers—Brazil: *Sellow 7769* (BM), *Lindeman & De Haas 2543* (BM).

Dyssochroma viridiflora (Sims) Miers—Brazil: *Anon s.n.* (BM), *Mello Barreto 1822* (K); *Pits 1894* (K).

Juanulloa ferruginea Cuatrecasas—Peru: *Vásquez, Jaramillo, Arévalo & López 4305* (NY), *Encarnación 1285* (NY).

Juanulloa globifera (S. Knapp & D'Arcy) S. Knapp—Colombia: *Cogollo, Ramírez & Alvarez 2895* (JAUM).

Juanulloa membranacea Rusby—Bolivia: *Britton & Rusby s.n.* (BM).

Juanulloa mexicana (Schltdl.) Miers—Colombia: *Lawrance s.n.* (BM); Costa Rica: *Anon s.n.* (BM); Mexico: *Cedillo & Calzada 133* (BM).

Juanulloa ochracea Cuatrecasas—Colombia: *Schultes & Cabrera s.n.* (BM); Ecuador: *Baker & Trusher 6118* (NY); Peru: *Ayala, Vásquez, Torres & Calderón s.n.* (NY), *Klug 2360* (K).

Juanulloa parasitica Ruiz & Pavón—Bolivia: *Nee & Coimbra 40085* (NY); Peru: *Foster 9924* (NY), *Plowman & Schunke V. 11765* (K).

Juanulloa pavonii (Miers) Benth. & Hook.—Ecuador: *Pavon s.n.* (BM), *Plowman & Alcorn 14351* (NY); Peru: *Simpson & Schunke 427* (NY).

Juanulloa speciosa (Miers) Dunal—Colombia: *Luteyn, Dumont & Buritica 4884* (NY), *Anon s.n.* (BM).

Juanulloa verrucosa (Rusby) Hunz.—Bolivia: *Steinbach 8466* (BM).

Juanulloa wardiana (D'Arcy) S. Knapp—Panama: *McDonagh, Lewis, Gumpel & Plumptre 251* (BM), *Luteyn 4096* (NY).

Markea camponoti Ducke—Brazil: *Daly, Campbell, Silva, da Silva, Bahia & dos Santos D879* (NY), *Guèdes s.n.* (BM); Guyana: *Bartlett 5414* (K).

Markea coccinea L. C. Richard—Brazil: *Egler 47679* (NY), *Mori, Mora Cardoso, deSilva & Sothers 20215* (NY); Colombia: *Schultes & Cabrera s.n.* (BM); Guyana: *Myers 5953* (K); Peru: *Foster, Fernández & Vivar 10766* (NY).

Markea costanensis Steyerm.—Venezuela: *Steyermark & Davidse 116312* (NY), *Steyermark & Davidse 116951* (NY).

Markea formicarum Ducke—Peru: *Ayala, Vásquez, Torres & Calderón 2563* (NY); Venezuela: *Nee 30923* (NY).

Markea lopezii Hunz.—Colombia: *Croat 50164* (MO), *Gentry, Juncosa & Gomez 40820* (NY).

Markea panamensis Standl.—Colombia: *Forero, Jaramillo & Lean 1606* (NY); Panama: *de Nevers, Herrera & Charnley 5041* (K), *Gentry 8761* (NY), *Kirkbride & Briston 1454* (NY), *McDonagh, Lewis, Gumpel & Plumptre 101* (BM).

Markea sessiliflora Ducke—Guyana: *Anon 3974* (K), *Jenman 633* (K), *Pipoly 7556* (NY); Brazil: *Ducke s.n.* (BM).

Markea ulei (Dammer) Cuatr.—Peru: *Vásquez & Jaramillo 9647* (NY), *Ramos & Lima 17170* (NY).

Merinthopodium neuranthum (Hemsl.) Donn. Sm.—Belize: *Hazlett & Coe 2748* (NY), *Peck 508* (NY); Colombia: *Sánchez, Orrego, Sylva, Martinez, Restrepo & Bahamon 1559* (NY); Costa Rica: *Wilbur & Stone 10091* (NY); Nicaragua: *Gomez 21033* (MO), *Moreno 23392* (MO); *Stevens & Krukoff s.n.* (BM); Panama: *Hammel 6096* (NY), *McPherson & Aranda 10175* (BM); Venezuela: *Luteyn, Lebron-Luteyn, Ruíz-Terán & Dugarte 5354* (BM).

Schultesianthus coriaceus (Kuntze) Hunz.—Colombia: *Nee & Callejas 32545* (NY), *Tracey s.n.* (K), *Zarucchi, Brant & Betancour 6034* (NY).

Schultesianthus crosbianus (D'Arcy) S. Knapp—Costa Rica: *Davidse, Herrera & Grayum 28688* (NY); Panama: *Folsom, Channell, Dressler & Dressler 7117* (MO), *de Nevers & Charnley 6058* (BM).

Schultesianthus dudleyi Bernardello & Hunz.—Ecuador: *Madsen 86180* (NY), *Madsen & Elleman 75160* (BM).

Schultesianthus leucanthus (Donn. Sm.) Hunz.—Panama: *Hampshire & Whitefoord 469* (BM).

Schultesianthus megalandrus (Dunal) Hunz.—Costa Rica: *Haber & Cruz 8402* (BM), *Herrera 502* (BM); Venezuela: *Steyermark & Steyermark 9529* (K).

Schultesianthus uniflorus (Lundell) S. Knapp—Mexico: *Breedlove & Smith 31710* (MO).

Schultesianthus venosus (Standley & C. V. Morton) S. Knapp—Costa Rica: *Grayum, Haufler & Rous 7755* (NY); Panama: *Hampshire & Whitefoord 856* (BM).

Solandra boliviana Britton—Bolivia: *Gentry & Solomon 52048* (NY), *Croat 51550* (MO).

Solandra brachycalyx Kuntze—Costa Rica: *Lankester s.n.* (K); Panama: *Hammel 7360* (BM).

Trianaea brevipes (Cuatr.) S. Knapp—Ecuador: *Palacios & van der Werff 3673* (NY).

Trianaea naeka S. Knapp—Ecuador: *Neill & Cerón 7449* (NY).

Trianaea neovisae Romero-Castañeda—Peru: *Díaz & Osores 2944* (MO).
Trianaea nobilis Planch. & Linden—Colombia: *Silverstone-Sopkin 1188* (MO); Ecuador: *Zak 1028* (K).
Trianaea speciosa (Drake) Soler.—Ecuador: *Boeke 547* (NY), *Gentry, Bonifaz & Loor 30950* (MO), *Dodson & Dodson 18592* (NY); *Spruce 5527* (K); Peru: *Barbour 4113* (MO).
Trianaea sp. nov.—Peru: *Díaz, Osores & Bustamente 3935* (MO).

A REVISION OF THE GENUS *XIPHOTHECA* (FABACEAE)[1]

Anne Lise Schutte[2]

Abstract

The genus *Xiphotheca* Eckl. & Zeyh. consists of nine species, all endemic to the Flora Capensis region of South Africa: *X. canescens, X. cordifolia, X. elliptica, X. fruticosa, X. guthriei, X. lanceolata, X. phylicoides, X. reflexa,* and *X. tecta.* Morphological, chemical, and cytological characters of the genus are briefly discussed. A cladistic analysis, based on morphological data, shows that there are two distinct groups in the genus. These are described as two sections, sects. *Congestae* and *Xiphotheca.* Full descriptions, diagnostic characters, illustrations, and distribution maps of the species are presented.

When De Candolle (1825a, b, 1826) described the genus *Priestleya,* he established two sections: *P.* sect. *Aneisothea* (with the calyx base attenuate) and *P.* sect. *Priestleya* (with the calyx base intrusive or "thrust in"). In 1836, Ecklon and Zeyher constituted the genus *Xiphotheca* by according generic status to *P.* sect. *Aneisothea.* This concept was not accepted by their successors (Meyer, 1836; Walpers, 1839; Bentham, 1843, 1865; Harvey, 1862; Hutchinson, 1964), who chose to follow De Candolle's classification. Recently, however, Schutte and Van Wyk (1993) offered additional evidence in support of Ecklon and Zeyher's (1836) concept and subsequently reinstated the genus *Xiphotheca.* The name *Xiphotheca* is a compound word, derived from the Greek words "xipho-" meaning sword-like and "-theca" meaning case or container, which refers to the shape of the pod.

Xiphotheca is a genus of papilionoid legumes comprising nine species, which are all endemic to the Cape fynbos region of South Africa. It is a member of the tribe Liparieae, which differs from the closely related tribe Podalyrieae in the fusion of the stamens into an open sheath or a closed tube. The Podalyrieae have the stamens free almost to the base (Polhill, 1976, 1981a, b). In a recent phylogenetic analysis of relationships between the genera of the Podalyrieae and Liparieae, Van Wyk and Schutte (1995) showed that *Xiphotheca, Amphithalea* Eckl. & Zeyh., and *Coelidium* Vogel ex Walp. are undoubtedly monophyletic, but that more research is needed to clarify the positions of some of the other genera. Data, gained from chemical investigations, have brought new insights into the relationships between the two tribes. The results of this investigation will be published elsewhere.

The diagnostic characters of *Xiphotheca* are the relatively unspecialized bright yellow flowers; the decussate, 2-flowered inflorescences; the non-intrusive calyx base (except for one species); the fusion of the bract with the base of the pedicel; the presence of bracteoles (albeit sometimes strongly reduced); the laterally compressed pods, which are constricted between the seeds; and the presence of anabasine as a major alkaloid. From its closest relatives, *Amphithalea* and *Coelidium,* it differs in the shape of the seed aril, which lacks the extension toward the lens; the generally higher ovule number; and the absence of ammodendrine as a major alkaloid.

Apart from a brief synopsis, in which the nomenclature, synonymy, and typification of the species are discussed (Schutte & Van Wyk, 1993), no taxonomic treatment of the group has been published since Harvey's in 1862. The aim of this paper is to present a revision of *Xiphotheca,* in which a phylogeny is proposed for the genus, followed by an identification key, full descriptions, illustrations, and distribution maps of the species.

Materials and Methods

Data on the morphological variation of the taxa were gathered from herbarium collections of BM, BOL, C, G, G-DC, JRAU, K, LD, LINN, MO, NBG, P, PRE, S, SAM, SBT, TCD, UPS, W, WU, and Z

[1] This study formed part of a Ph.D. thesis in Botany at the Rand Afrikaans University. I am indebted to B.-E. van Wyk for supervising the study. The directors and staff of the mentioned herbaria are thanked for loans of specimens. My husband, J. H. J. Vlok (Cape Nature Conservation), kindly offered advice and assistance during collecting trips. Financial support from the Foundation for Research Development is acknowledged.

[2] Department of Botany, Rand Afrikaans University, P.O. Box 524, 2006 Auckland Park, Johannesburg, Republic of South Africa. Present address: Compton Herbarium, National Botanical Institute, Private Bag X7, 7735 Claremont, Republic of South Africa.

(acronyms as in Holmgren et al., 1981), as well as from fresh or preserved material collected during field trips.

The methods applied in the alkaloid study are described by Van Wyk et al. (1991a, b). Voucher specimens of the material used for the extraction of alkaloids are also listed.

Cladograms were generated by using the computer software package Hennig 86 (Farris, 1988). Character states were polarized using the method of outgroup comparison. It is important to note that autapomorphies for the different species have been omitted from the analysis, since they serve no purpose as grouping characters. The "mhennig*," "bb*," and "ie" algorithms were applied to produce trees of minimal length.

Morphological Characters

HABIT

The variation in habit found in *Xiphotheca* includes single-stemmed, tree-like shrubs up to 2.5 m tall, many-stemmed, virgate shrubs up to 1.2 m tall, and prostrate or straggling shrublets of up to 0.5 m tall. Adaptations to survive recurrent fires have had a major influence on the life forms and habit of the taxa, since all are restricted to the fire-prone fynbos vegetation of the Cape (Le Maitre & Midgley, 1992; Schutte et al., 1995). There are two main fire survival strategies: sprouters and non-sprouters. Sprouters have a lignotuber from which new growth takes place after fire, resulting in a many-stemmed appearance at ground level. Non-sprouters, on the other hand, can only reproduce from seed after fire and are easily recognized by the presence of a single main stem, at least at ground level (Schutte et al., 1995).

At the specific level, the ability to resprout or reseed after fire is a taxonomically important and very useful character in *Xiphotheca*. For example, *X. canescens* (Thunb.) A. L. Schutte & B.-E. van Wyk and *X. elliptica* (DC.) A. L. Schutte & B.-E. van Wyk look morphologically very similar, especially on herbarium sheets, but have different fire-survival strategies.

Fire survival strategy is not included as a character in the cladistic analyses because it is a polymorphic character. In *X. fruticosa*, some populations are sprouters, while other populations consist of non-sprouting individuals.

LEAVES

All the species of *Xiphotheca* have simple, petiolate, and distinctly pinnately veined leaves. Stipules are invariably present, but reduced in size. Leaves are generally flat, except in *X. phylicoides* A. L. Schutte & B.-E. van Wyk, where the margins are strongly revolute. The vestiture of the leaves varies among the species from pubescent to sericeous to tomentose or velutinous, and some of the species can be identified by their leaf indumentum.

INFLORESCENCES

Xiphotheca has axillary, simple racemose inflorescences, with geminate flowers. At the infrageneric level, inflorescences are particularly useful in distinguishing between some of the species. In *X. canescens, X. cordifolia* A. L. Schutte & B.-E. van Wyk, *X. elliptica*, and *X. phylicoides*, the inflorescences are distinctly pedunculate. They are either borne on lateral twigs, as in *X. canescens, X. cordifolia*, and *X. elliptica*, or borne on the main stem as in the remainder of the species. In *X. fruticosa* (L.) A. L. Schutte & B.-E. van Wyk, *X. guthriei* (L. Bolus) A. L. Schutte & B.-E. van Wyk, *X. lanceolata* (E. Mey.) Eckl. & Zeyh., and *X. reflexa* (Thunb.) A. L. Schutte & B.-E. van Wyk, the inflorescence-supporting leaves are smaller than the other vegetative leaves and the inflorescence units are congested. The flowers are totally concealed by the leaves below the inflorescence units in *X. guthriei* and *X. lanceolata*. All the species have the bracts fused with the pedicel at the base for a distance of 0.5 to 1.0 mm. Bracteoles are conspicuous in *X. canescens, X. elliptica*, and *X. phylicoides*, strongly reduced in *X. cordifolia, X. reflexa*, and *X. tecta* (DC.) A. L. Schutte & B.-E. van Wyk, and absent in the other species.

FLOWERS

Calyx. An attenuate calyx base is characteristic of *Xiphotheca*. There is, however, one species that has an intrusive calyx base (Schutte & Van Wyk, 1993), but it is here regarded as a secondary development. The upper two calyx lobes are invariably fused higher up than the lower three lobes. *Xiphotheca fruticosa, X. guthriei, X. lanceolata*, and *X. reflexa* are exceptional in having the carinal calyx lobe notably longer than the other lobes. The shape of the calyx lobes is a significant taxonomic character that varies from narrowly triangular and acuminate to rounded and obtuse.

Corolla. The corolla is yellow and relatively unspecialized in *Xiphotheca* and tends to turn brown with age. Keel petals are obtuse, distinctly pocketed, and auriculate. The pocket on the wing petal is a thickened lobe, formed on the inside (ab-

axial side), but *X. tecta* is unusual in having a well-developed pocket conspicuous also on the adaxial side. Wing petal sculpturing is invariably present in the upper basal area. The wing auricle is well differentiated in *X. canescens* and *X. elliptica*, but weakly so in the other species.

Stamens. In *Xiphotheca* the stamens are diadelphous and the anthers almost uniform in shape and size. The mode of attachment of the filaments is alternately dorsifixed and subbasifixed.

Pistils. The number of ovules varies from two to eight in the genus. These differences are useful in distinguishing between some species.

FRUITS AND SEEDS

The significance of fruit characters as a taxonomic character for *Xiphotheca* is obvious; the generic name alludes to the shape of the pod. Pods are sessile, laterally compressed, and constricted between the seeds in *Xiphotheca*. The seeds are arillate and vary in color from uniformly green or brown to green, mottled brown and brown, mottled black.

CHROMOSOME NUMBER

Chromosome numbers of only three species have so far been recorded: *X. fruticosa*, *X. guthriei*, and *X. tecta*. All have $2n = 18$ (Dahlgren, 1967; Schutte, 1995). A basic chromosome number of $x = 9$ seems likely. This is in accordance with the proposed base number for the tribe Liparieae (Goldblatt, 1981).

ALKALOIDS

Alkaloids have proved to be of great significance at the generic level. In fact, it was one of the most convincing characters used to motivate the reinstatement of *Xiphotheca* as a genus (Schutte & Van Wyk, 1993). The major alkaloids detected in *Priestleya* DC. sect. *Aneisothea* DC. (now *Xiphotheca*) were anabasine (a bipiperidyl alkaloid) and lupinine (a bicyclic quinolizidine alkaloid), while a combination of lupanine- and sparteine-type alkaloids (all tetracyclic quinolizidine alkaloids) and minor quantities of ammodendrine (a bipiperidyl alkaloid) were located in *Priestleya* sensu stricto (Van Wyk et al., 1991b). This offered additional support to morphological evidence that *Priestleya* is paraphyletic, which subsequently resulted in the reinstatement of *Xiphotheca* (Schutte & Van Wyk, 1993). At the specific level, no clear pattern in variation could be found, since the differences were of a quantitative, rather than a qualitative, nature.

Table 1. Characters and character states used for the cladistic analysis of the genus *Xiphotheca*. The fully resolved cladogram generated from this data set is shown in Figure 1.

Taxa	Character states
AMPHITHALEA	00000 00000 0
X. canescens	01101 11001 1
X. cordifolia	01101 1000? 1
X. elliptica	01101 11001 1
X. fruticosa	10010 00100 0
X. guthriei	10020 00110 0
X. lanceolata	10020 00110 0
X. phylicoides	01001 10000 0
X. reflexa	10010 10110 1
X. tecta	01000 10000 1

Characters

1. Inflorescence supporting leaves: similar to others (0); reduced in size (1).
2. Inflorescence units: congested (0); not congested (1).
3. Inflorescences: borne on main stems (0); borne on lateral twigs (1).
4. Inflorescences: not concealed by leaves below inflorescence units (0); partly concealed by leaves below inflorescence units (1); totally concealed by leaves below inflorescence units (2).
5. Peduncles: absent (0); present (1).
6. Bracteoles: absent (0); present (1).
7. Calyx lobes: acuminate (0); not acuminate (1).
8. Calyx lower lobe: as long as the others (0); longer than the other lobes (1).
9. Vestiture: pubescent (0); not pubescent (1).
10. Wing petals: auricle weakly developed or absent (0); distinctly auriculate (1).
11. Ovule number: 2 (0); more than 2 (1).

INFRAGENERIC RELATIONSHIPS

Xiphotheca is defined by at least three unambiguous apomorphies and one subject to variation: (1) the presence of bracteoles in most species; (2) the fusion of the bracts with the base of the pedicel; (3) the laterally compressed pods; and (4) the accumulation of anabasine as a major alkaloid.

For the phylogenetic analysis, *Amphithalea* was chosen as outgroup, since it is the genus most closely related to *Xiphotheca* (Van Wyk & Schutte, 1995). A data set was compiled using 10 taxa and 11 characters (Table 1). Two fully resolved trees resulted, both with a length of 15 and a consistency index of 80. The one most favored is shown in Figure 1. In the other tree the positions of *X. tecta* and *X. phylicoides* are switched. The cladogram indicates two major clades: a *Xiphotheca guthriei*-group (A), subtended by three synapomorphies, and a *Xiphotheca canescens*-group (B) supported by one apomorphy. These two infrageneric groups are given formal taxonomic rank below.

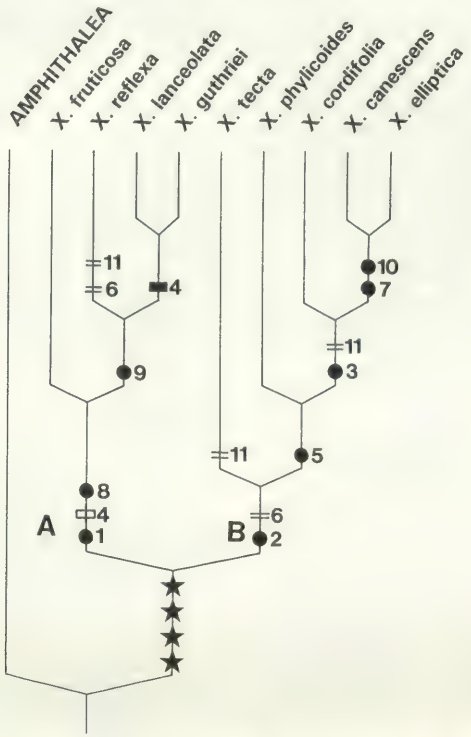

Figure 1. Fully resolved cladogram of relationships in the genus *Xiphotheca*, based on the data set in Table 1 [dot, an apomorphy without homoplasy; rectangle, an apomorphy with subsequent reversal or successive states of a multistate character; =, a convergence; stars, generic apomorphies (see text)].

Taxonomic Treatment

Xiphotheca Eckl. & Zeyh., Enum. Pl. Afric. Austral. 2: 166. 1836. TYPE: *Xiphotheca rotundifolia* Eckl. & Zeyh. (lectotype, designated by Schutte & Van Wyk, 1993) [= *Xiphotheca tecta* (Thunb.) A. L. Schutte & B.-E. van Wyk].

Priestleya DC. sect. *Aneisothea* DC., in Ann. Sci. Nat. 4: 91. 1825, Prodr. 2: 121. 1825. TYPE: *Priestleya elliptica* DC. (lectotype, designated by Schutte & Van Wyk, 1993) [= *Xiphotheca elliptica* (DC.) A. L. Schutte & B.-E. van Wyk].

Woody shrubs or shrublets. *Leaves* alternate or rarely opposite or subopposite, simple, narrowly elliptic to almost circular, mostly flat, sometimes with recurved margins, pinnately veined; petiole short, ± 1 mm long; stipules inconspicuous, less than 0.5 mm long. *Inflorescence* axillary, 2-flowered, with the two flowers opposite, aggregated into synflorescences of up to 20 flowers. *Bracts* linear to oblanceolate, fused at the base with pedicel for 0.5–1.0 mm. *Bracteoles* minute, sometimes lacking. *Corolla* yellow, longer than the calyx, glabrous. *Calyx* narrowed to the base, rarely intrusive; upper two lobes fused higher up than the lower three lobes; carinal lobe sometimes longer than the upper four. *Standard petal* suborbicular to elliptic; apex emarginate. *Wing petals* oblong, longer than the keel; the tips imbricate; pocket developed as a thickened lobe toward the inside. *Keel petals* widely obovate, with weakly developed pockets, apex obtuse. *Stamens* diadelphous, the vexillary filament free; anthers ± uniform in shape and size, alternately dorsifixed and subbasifixed. *Pistil* sessile; style slender,

slightly upcurved, glabrous; ovary with 2 or more ovules, densely sericeous to tomentose. *Pods* coriaceous, usually linear, sometimes obliquely oblong, laterally compressed, constricted between the seeds, 2 to many seeded, densely pubescent, tomentose, villous or glabrous. *Seeds* oblong-reniform; hilum elliptic, surrounded by a fleshy collar-like aril. Chromosome number $2n = 18$. Nine species.

Xiphotheca is restricted to the fynbos region of the Western and Northern Cape Provinces.

KEY TO THE SPECIES OF *XIPHOTHECA*

1. Leaves opposite; calyx base intrusive ..... 7. *X. cordifolia*
1. Leaves subopposite or alternate; calyx base not intrusive 2
2(1). Inflorescences pedunculate 3
2. Inflorescences not pedunculate 5
3(2). Ovary with 2 ovules ..... 5. *X. phylicoides*
3. Ovary with 5 or more ovules 4
4(3). Leaves elliptic, with slightly revolute margins; many-stemmed shrubs up to 1 m tall; pods densely pubescent ..... 9. *X. elliptica*
4. Leaves narrowly elliptic, with flat margins; single-stemmed tree-like shrubs up to 2.5 m tall; pods ± glabrous ..... 8. *X. canescens*
5(2). Ovary with 5 or more ovules 6
5. Ovary with 2 or 3 ovules 7
6(5). Wing petal with pocket conspicuous on outer surface; calyx shorter than keel, lobes triangular, tomentose; seeds green, not mottled ..... 6. *X. tecta*
6. Wing petal with pocket not conspicuous on outer surface; calyx ± as long as the keel, lobes narrowly triangular, villous; seeds brown, mottled black ..... 2. *X. reflexa*
7(5). Lower calyx lobe much longer than the tube ..... 3. *X. lanceolata*
7. Lower calyx lobe as long as or shorter than the tube 8
8(7). Leaves elliptic, silver, densely sericeous (long silky appressed hairs) on both surfaces; bracts 5–9 mm long; seeds pale greenish brown, mottled dark brown ..... 1. *X. fruticosa*
8. Leaves narrowly elliptic, green, sparsely velutinous (long soft upright hairs) on both surfaces, densely so on margins; bracts ± 2.5 mm long; seeds uniformly brown ..... 4. *X. guthriei*

Section 1. Xiphotheca sect. **Congestae** A. L. Schutte, sect. nov. TYPE: *Xiphotheca reflexa* (Thunb.) A. L. Schutte & B.-E. van Wyk.

Sectioni *Xiphothecae* similis, sed inflorescentiis partialibus congestis et lobo calycis carinali longiori differt.

Section *Congestae* is similar to section *Xiphotheca* but deviates in its congested inflorescence units and in the carinal lobe of the calyx that is longer than the upper four lobes. This section comprises four species.

1. Xiphotheca fruticosa (L.) A. L. Schutte & B.-E. van Wyk, Taxon 42: 46. 1993. *Lotus fruticosus* L., Syst. Nat. (ed. 10): 1179. 1759. TYPE: South Africa. Western Cape, without locality, *Anon. s.n.* (lectotype, designated by Schutte & Van Wyk (1993), S, Linnaeus Type Herb. No. S293.5).

Crotalaria lanata Thunb., Prodr. Pl. Cap.: 124. 1800. TYPE: South Africa. Western Cape, "e Cap. b. Spei," *Thunberg s.n.* (lectotype, designated by Schutte & Van Wyk (1993), UPS, Herb. Thunberg No. 16557).

Priestleya villosa DC., Prodr. 2: 122. 1825, *nom. illeg. Xiphotheca villosa* (DC.) Eckl. & Zeyh., Enum. Pl. Afric. Austral. 2: 166. 1836. TYPE: South Africa. Western Cape, "Cap. de B. Esp.," *Lambert s.n.* (lectotype, designated by Schutte & Van Wyk (1993), G-DC).

Single-stemmed, tree-like shrub up to 2 m tall, not sprouting after fire, or sometimes, a many-stemmed shrub up to 0.7 m tall, sprouting after fire; woody rootstock sometimes present. *Leaves* alternate, elliptic, flat, silvery, densely sericeous on both surfaces, glabrescent. *Inflorescences* aggregated into head-like synflorescences at tips of main branches, somewhat concealed by supporting leaves; peduncle absent. *Bracts* narrowly elliptic to linear, 5–9 mm long. *Pedicel* 2.5–3.0 mm long. *Bracteoles* absent. *Calyx* not intrusive at base; lobes acuminate, shorter than the tube; carinal lobe slightly longer than upper four; densely sericeous. *Wing petals* auriculate; pocket inconspicuous on outer surface. *Ovary* with 2 to 3 ovules; densely tomentose. *Pods* inflated; tomentose. *Seeds* pale greenish brown, mottled dark brown. Figure 2.

Xiphotheca fruticosa is found on the Cape Peninsula-, Hottentotsholland-, Hex River-, and Touwsberg Mountains, as well as on the mountains near Montagu and hills near Bredasdorp (Fig. 3). It grows in a sandy loamy soil at altitudes of 100 to 1200 m.

This species resembles *X. guthriei* but differs in longer bracts and long silky appressed, not velutinous, hairs on the leaves.

Both sprouting and non-sprouting growth forms occur in this species. Populations from the Bredasdorp-Elim area resprout after fire, while those from the other localities do not. This difference in growth form may be significant, but more fieldwork is needed before specific or infraspecific status can be assigned with certitude.

Selected specimens examined. **Non-sprouting form:** SOUTH AFRICA. Cape Peninsula: Noord Hoek Mountain, *Barker 2080* (NBG). Cape Town: Devil's Peak, *Bolus 3765* (SAM). Simons Town: Chapman's Peak, *Pillans s.n.*

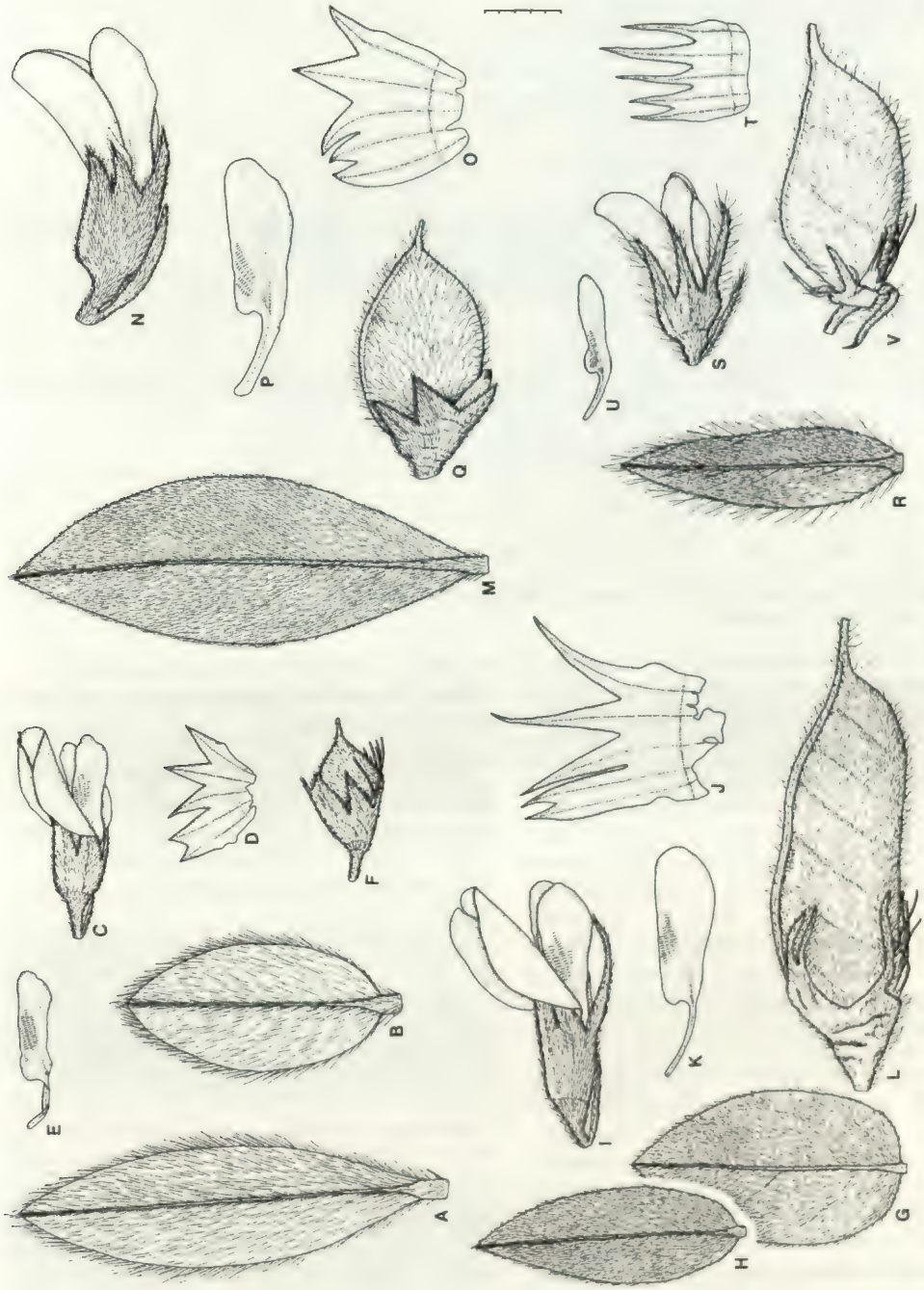

Figure 2. A–F. *Xiphotheca guthriei*. G–L. *X. reflexa*. M–Q. *X. fruticosa*. R–V. *X. lanceolata*. A, B, G, H, M, R: leaves, abaxial view; C, I, N, S: flowers in lateral view; D, J, O, T: calyces (upper lobes to the left); E, K, P, U: wing petals; F: immature fruit; L, Q, V: mature fruits. A: *Vlok & Schutte 4*; B, D, F: *Guthrie 3866*; C, E: *Oliver 4288*; G, H: *Bolus 3697*; I, J, K: *Luckhoff s.n.*; L: *Taylor 6039*; M: *Schutte 720*; N, O, P: *Schutte 675*; Q: *anon. 130*; R, T, U: *Pillans 6264*; S: *Barker 1644*; V: *Boucher 3393*. Scale in mm.

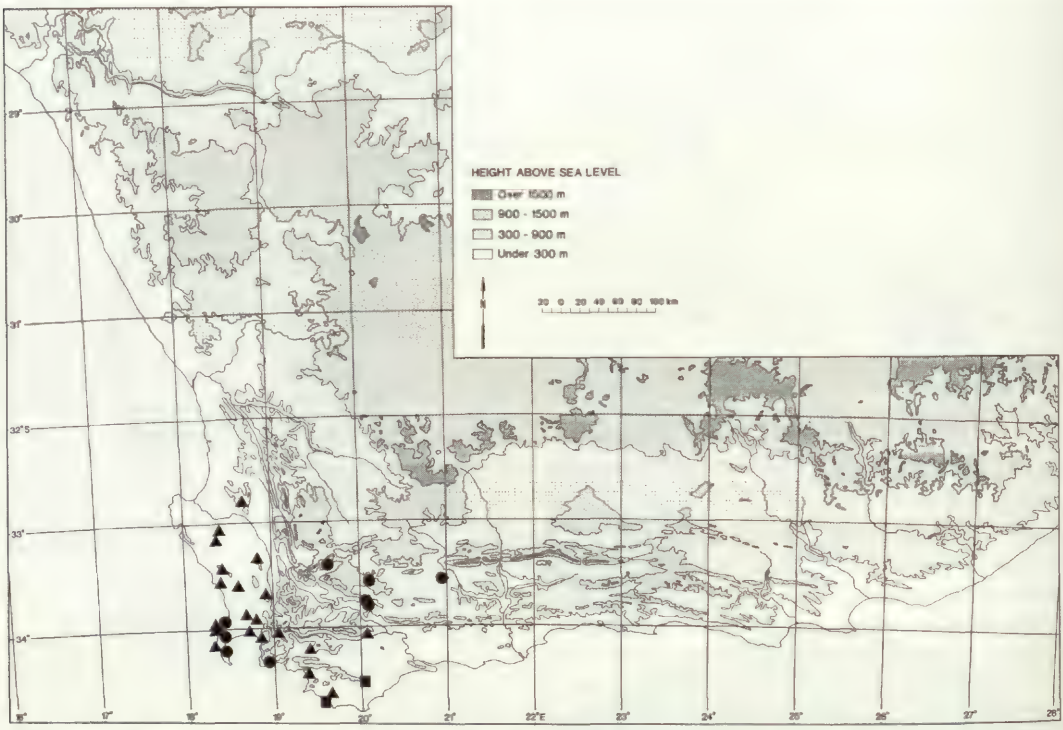

Figure 3. The known geographical distribution of *Xiphotheca fruticosa* (dots, non-sprouting form; squares, resprouting form) and *X. reflexa* (triangles).

(BOL 51233). Montagu: Pypsteelfontein, *Schutte 673–675* (JRAU). Ladismith: Touwsberg, *Vlok & Schutte 155* (MO). **Sprouting form:** SOUTH AFRICA. Elim: Koueberge, kloof above Nuwepos, *Oliver 5854* (NBG, PRE). Bredasdorp: upper slopes of mountain above Bredasdorp, *Burgers 2708* (NBG, PRE), *Vlok & Schutte 365* (MO).

2. Xiphotheca reflexa (Thunb.) A. L. Schutte & B.-E. van Wyk, Taxon 42: 47. 1993. *Crotalaria reflexa* Thunb., Prodr. Pl. Cap.: 125. 1800. TYPE: South Africa. Western Cape, "e Cap. b. Esp." *Thunberg s.n.* (lectotype, designated by Schutte & Van Wyk (1993), UPS, Herb. Thunberg no. 16576).

Many-stemmed prostrate to straggling shrub up to 0.5 m tall, sprouting from a woody rootstock after fire. *Leaves* alternate, ovate to lanceolate, flat, densely sericeo-tomentose on both surfaces, glabrescent. *Inflorescences* scattered along main branches, partly concealed by supporting leaves; peduncle absent. *Bracts* linear, 5–8 mm long. *Pedicel* 2.5–3.0 mm long. *Bracteoles* minute, caducous. *Calyx* not intrusive at base; lobes acuminate, much longer than the tube; carinal lobe longer than the upper four, almost as long as the keel petals; densely sericeous. *Wing petals* auriculate; pocket inconspicuous on outer surface. *Ovary* with 5–7 ovules; densely sericeous. *Pods* laterally compressed; densely villous. *Seeds* brown, mottled black. Figure 2.

This species is also restricted to the southwestern Cape, from the Piquetberg in the north southeastward to the Caledon-Elim region in the south (Fig. 3). *Xiphotheca reflexa* is usually found at low altitudes (less than 300 m), growing in deep sandy soils.

Characters distinguishing *X. reflexa* from *X. lanceolata* are the sericeo-tomentose leaves and the several-seeded (5–7) pods. *Xiphotheca lanceolata* has a densely appressed-sericeous vestiture on the leaves, with rather stiff hairs on the margins and midrib and 2- or 3-seeded pods.

Selected specimens examined. SOUTH AFRICA. Malmesbury: Farm Bokbaai near Darling, *Barker 10589* (NBG). Stellenbosch: Bottelary, *Compton 12935* (NBG). Malmesbury: near Hopefield, *Compton 18928* (NBG). Cape Town: lower slopes of Table Mountain, *Esterhuysen 15637* (BOL). Cape Peninsula: Oranjezicht, *Penfold 98* (NBG).

3. Xiphotheca lanceolata (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afric. Austral. 2: 167. 1836. *Priestleya lanceolata* E. Mey., Linnaea 7: 150. 1832. TYPE: South Africa. Western Cape,

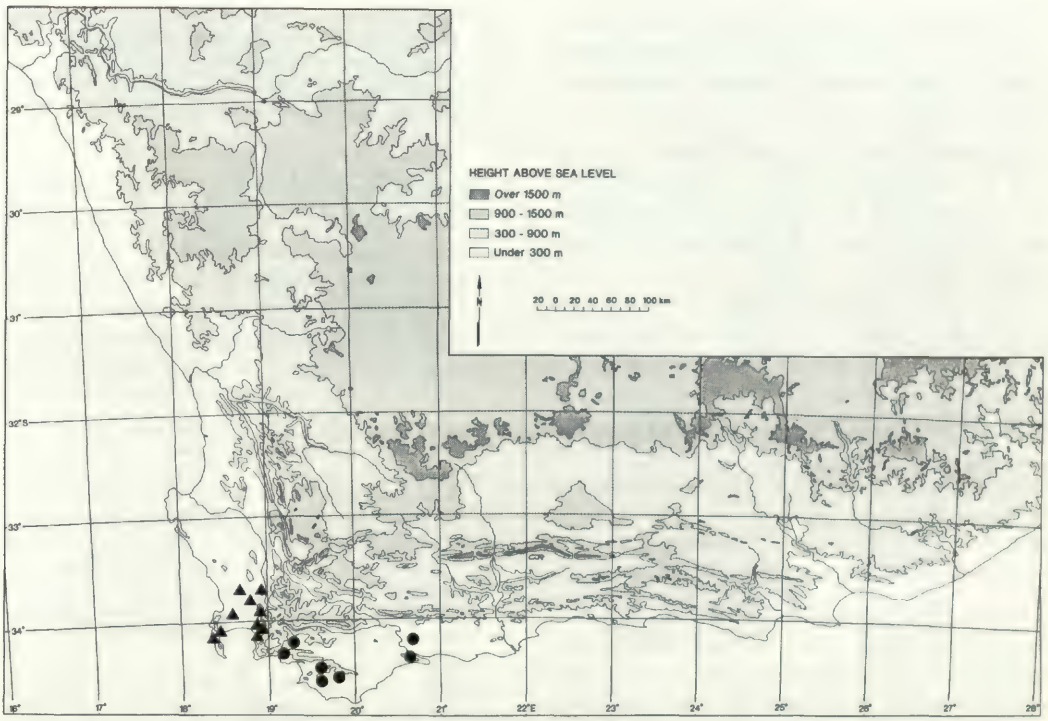

Figure 4. The known geographical distribution of *Xiphotheca lanceolata* (triangles) and *X. guthriei* (dots).

"Kapsche Fläche bei Constantia," *Ecklon s.n.* (lectotype, designated by Schutte & Van Wyk (1993), S).

Priestleya glauca T. M. Salter, J. S. Afr. Bot. 8: 256. 1942. TYPE: South Africa. Western Cape, on lower slopes of Hercules' Pillar, Joostenberg, *Pillans 6264* (lectotype, designated by Schutte & Van Wyk (1993), BOL; isolectotypes, K, NBG).

Single-stemmed shrublet up to 0.6 m tall, not sprouting after fire; woody rootstock absent. *Leaves* alternate, narrowly elliptic, flat, densely appressed-sericeous on both surfaces with long, rather stiff hairs on margins and midrib, glabrescent. *Inflorescences* aggregated into head-like synflorescences at tips of main branches, almost completely concealed by supporting leaves; peduncle absent. *Bracts* linear, 5.5–6.0 mm long. *Pedicel* ± 1.5 mm long. *Bracteoles* absent. *Calyx* not intrusive at base; lobes acuminate, much longer than the tube; carinal lobe longer than the upper four; densely sericeous with long, rather stiff hairs on lobes and main veins. *Wing petals* auriculate; pocket inconspicuous on outer surface. *Ovary* with 2 or 3 ovules; hirsute. *Pods* laterally compressed; hirsute. *Seeds* pale brown, mottled dark brown. Figure 2.

Xiphotheca lanceolata is a rare species that occurs only on the granite hills in and around the Cape flats (Fig. 4), at altitudes between 60 and 200 m. It is seriously threatened by urban development.

See discussion under *X. reflexa.*

Selected specimens examined. SOUTH AFRICA. Stellenbosch: Faure, *Barker 4121* (NBG). Somerset West: Vergelegen, *Compton 6410* (NBG). Paarl: top of granite hill above Nooitgedacht, *Dahlgren & Strid 4109* (LD); Northern slopes of Joostenberg, *Pillans 6264* (BOL, NBG). Stellenbosch: Sir Louwry's Pass, *Stokoe s.n.* (SAM 64930).

4. Xiphotheca guthriei (L. Bolus) A. L. Schutte & B.-E. van Wyk, Taxon 42: 46. 1993. *Priestleya guthriei* L. Bolus, Ann. Bolus Herb. 4: 125. 1928. TYPE: South Africa. Western Cape, hills near Elim, *Guthrie 3866* (holotype, BOL).

Single-stemmed shrub up to 0.3 m tall, not sprouting after fire; woody rootstock absent. *Leaves* alternate, elliptic to narrowly elliptic, flat, velutinous on both surfaces, glabrescent. *Inflorescences* aggregated into head-like synflorescences at tips of main branches, almost completely concealed by supporting leaves; peduncle absent. *Bracts* linear, ± 2.5 mm long. *Pedicel* ± 2 mm long. *Bracteoles* absent. *Calyx* not intrusive at base; lobes triangular acuminate, ± as long as the tube; carinal lobe as long as lateral lobes; velutinous. *Wing petals* not

auriculate; pocket inconspicuous on outer surface. *Ovary* with 2 ovules; densely sericeo-tomentose. *Immature pods* velutinous. *Immature seeds* uniformly brown. Figure 2.

Xiphotheca guthriei is limited to the surroundings of Bredasdorp, Elim, and Caledon (Fig. 4), where it grows in loamy, clayey soil at altitudes below 250 m. The survival of this species is threatened by farming.

See discussion under *X. fruticosa*.

Selected specimens examined. SOUTH AFRICA. Bredasdorp: Kourivier, between Napier and Stanford, *Jordaan 976* (C); Farm Klein Uintjieskuil just E of Viljoenshof, *Oliver 4288* (PRE). Heidelberg: hill N of Verkykerskop, *Schutte 760* (JRAU). Bredasdorp: ca. 3 km E of Viljoenshof, *Vlok & Schutte 4* (JRAU).

Section 2. Xiphotheca sect. **Xiphotheca**

This section differs from section *Congestae* in the extended flowering units, in the inflorescences, which are mostly pedunculate, and in the carinal calyx lobe, which is as long as the upper four lobes. It contains five species.

5. Xiphotheca phylicoides A. L. Schutte & B.-E. van Wyk, Taxon 42: 48. 1993. TYPE: South Africa. Oudtshoorn district, lower northern slopes of Outeniqua Mountains on farm Klein Moerasrivier, *Vlok 2640* (holotype, PRE; isotypes, B, BOL, JRAU, K, MO, NBG).

Many-stemmed shrub up to 1.2 m tall, sprouting from a woody rootstock after fire. *Leaves* alternate, elliptic to narrowly elliptic, with strongly revolute margins, sparsely sericeous on adaxial surface, soon becoming glabrous, densely sericeous on abaxial surface. *Inflorescences* borne along main branches; peduncle 1.5–2.5 mm long. *Bracts* linear to narrowly elliptic, 3–4 mm long. *Pedicel* 3.5–5.0 mm long. *Bracteoles* ± 0.5 mm long, caducous. *Calyx* not intrusive at base; lobes acuminate, ± as long as the tube; carinal lobe as long as lateral lobes; densely pubescent. *Wing petals* weakly auriculate; pocket inconspicuous on outer surface. *Ovary* with 2 ovules; densely pubescent. *Immature pods* laterally compressed; pubescent. *Seeds* unknown. Figure 5.

This species is known from only two localities on the Outeniqua Mountains near Mossel Bay (Fig. 6). *Xiphotheca phylicoides* is found in pebbly loamy soil at altitudes between 530 and 800 m.

The leaves of *X. phylicoides* are characteristic in having strongly revolute margins.

Specimens examined. SOUTH AFRICA. Oudtshoorn: lower northern slopes of Outeniqua Mountains on farm Klein Moerasrivier, *Schutte 801* (JRAU), *Vlok 2437* (JRAU), *2640* (B, BOL, JRAU, K, MO, NBG, PRE). Mossel Bay: Attaquaskloof Nature Reserve, *Vlok 2500* (JRAU).

6. Xiphotheca tecta (Thunb.) A. L. Schutte & B.-E. van Wyk, Taxon 42: 48. 1993. *Liparia tecta* Thunb., Prodr. Pl. Cap.: 124. 1800. *Priestleya tecta* (Thunb.) DC., Prodr. 2: 122. 1825. TYPE: South Africa. Western Cape, "Paardeberg, Picketberg, Hottentots Hollandberg," *Thunberg s.n.* (lectotype, designated by Schutte & Van Wyk (1993), UPS, Herb. Thunberg No. 17009; isolectotype, S).

Xiphotheca rotundifolia Eckl. & Zeyh., Enum. Pl. Afric. Austral. 2: 166. 1836. *Priestleya rotundifolia* (Eckl. & Zeyh.) Walp., Linnaea 13: 469. 1839. *Priestleya tecta* var. *rotundifolia* (Eckl. & Zeyh.) Harv., Fl. Cap. 2: 20. 1862. TYPE: South Africa. Western Cape, "In lapidosis laterum montium prope Waterfall in valle Tulbagh (Worcester)," *Ecklon & Zeyher 1224* (lectotype, designated by Schutte & Van Wyk (1993), S; isolectotype, S).

Xiphotheca polycarpa Eckl. & Zeyh., Enum. Pl. Afric. Austral. 2: 166. 1836. TYPE: South Africa. Western Cape, "In locis lapidosis laterum montium prope Klapmuts (Stellenbosch)," *Ecklon & Zeyher 1225* (lectotype, designated by Schutte & Van Wyk (1993), S; isolectotypes, S, W).

Priestleya stokoei L. Bolus, Ann. Bolus Herb. 4: 69. 1927. TYPE: South Africa. Western Cape, Stellenbosch division, foothills of mountains near Lourensford, Somerset West, *Stokoe 1375* (holotype, BOL).

Many-stemmed shrub up to 1 m tall, sprouting from a woody rootstock after fire. *Leaves* alternate, elliptic to almost circular, flat, often concave, densely pubescent to tomentose on both surfaces, glabrescent. *Inflorescences* borne along main branches; peduncle absent. *Bracts* linear, 2.5–7.5 mm long. *Pedicel* 2–4 mm long. *Bracteoles* minute, caducous. *Calyx* not intrusive at base; lobes acuminate to acute, slightly longer than the tube; carinal lobe as long as lateral lobes; densely pubescent. *Wing petals* not auriculate; pocket conspicuous on the outer surface. *Ovary* with 5–8 ovules; densely pubescent. *Pods* laterally compressed; densely tomentose. *Seeds* green, not mottled. Figure 5.

Xiphotheca tecta has a relatively wide distribution in the Western Cape, extending from Citrusdal in the north to Somerset West in the south (Fig. 6). It occurs on shale or granite soil at altitudes of 200 to 1350 m.

This species is unique in having a pocket on the wing petals that is conspicuous on the outer surface.

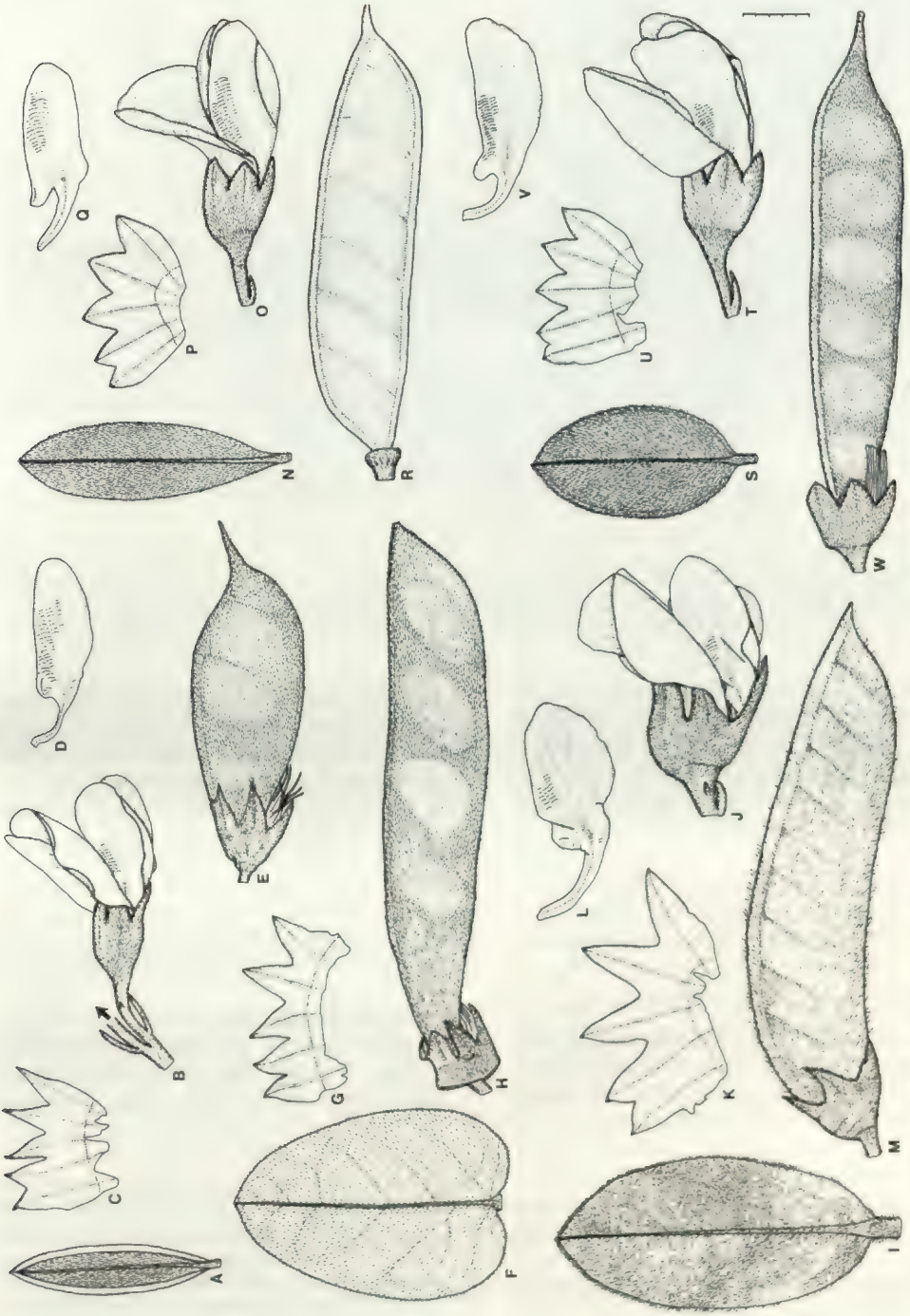

Figure 5. A–E, *Xiphotheca phylicoides*. F–H. *X. cordifolia*. I–M. *X. tecta*. N–R. *X. canescens*. S–W. *X. elliptica*. A, F, I, N, S: leaves, abaxial view; B, J, O, T: flowers in lateral view (note the presence of peduncle in B); C, G, K, P, U: calyces (upper lobes to the left); D, L, Q, V: wing petals; E, H, M, W: immature fruits; R: mature fruit. A–D: *Vlok 2640*; E: *Schutte 801*; F–H: *Esterhuysen 32556*; I–L: *Schutte 597*; M: *Schutte 767*; N–Q: *Vlok & Schutte 46*; R: *Stirton 11032*; S: *Grobbelaar 1176*; T–V: *Taylor 6930*; W: *Taylor 7217*. Scale in mm.

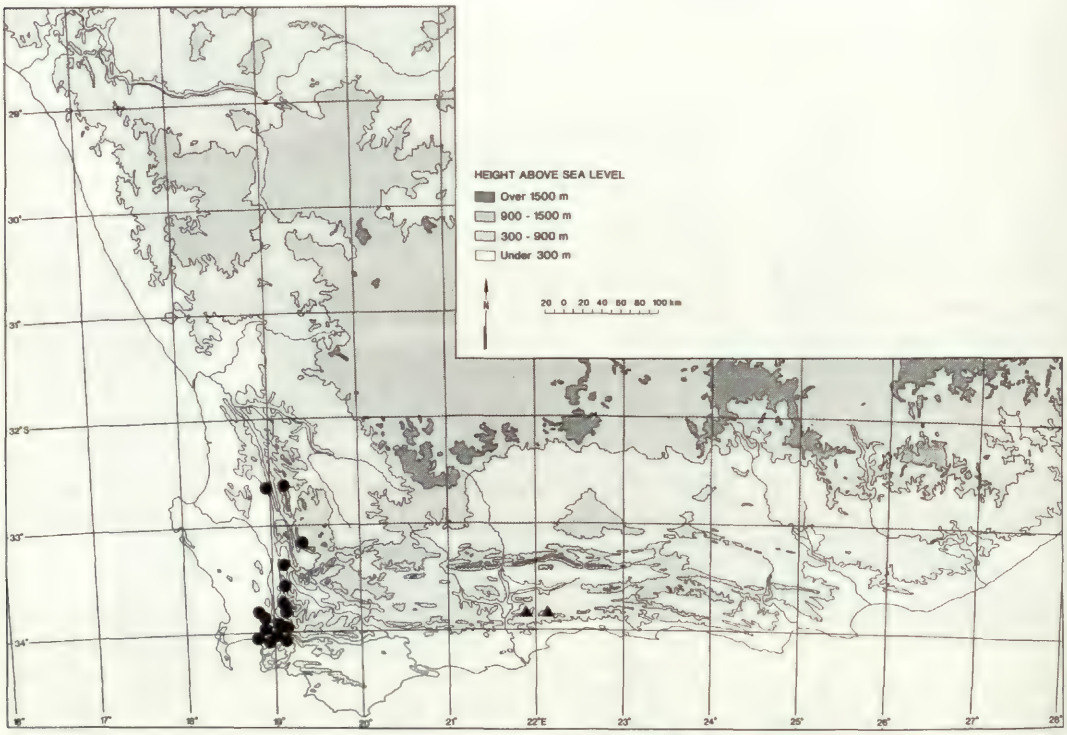

Figure 6. The known geographical distribution of *Xiphotheca tecta* (dots) and *X. phylicoides* (triangles).

Selected specimens examined. SOUTH AFRICA. Paarl: French Hoek Pass, *Bond 359* (NBG). Stellenbosch: Banhoek Valley, below the hut below Dragoon Buttress, *Esterhuysen 35653* (BOL). Citrusdal: Elandskloof Pass, *Schutte 701* (B, MO, JRAU). Paarl: Worcester side of Du Toitskloof Pass, *Schutte 714* (JRAU). Tulbagh: near Tulbagh Waterfall, *Stokoe 1399* (BOL).

7. Xiphotheca cordifolia A. L. Schutte & B.-E. van Wyk, Taxon 42: 48. 1993. TYPE: South Africa. Western Cape, Worcester district, Hex River Mountains, Milner Kloof, *Esterhuysen 31640* (holotype, BOL; isotypes, K, S).

Single-stemmed, tree-like shrub up to 2.5 m tall, not sprouting after fire; woody rootstock absent. *Leaves* opposite, cordate, flat, pubescent only on abaxial surface, glabrescent. *Inflorescences* borne at tips of lateral branches; peduncle 1.0–2.5 mm long. *Bracts* not seen. *Pedicel* 2.0–2.5 mm long. *Bracteoles* minute, caducous. *Calyx* intrusive at base; lobes acuminate, slightly longer than the tube; carinal lobe as long as lateral lobes; densely pubescent. *Wing petals* not seen. *Ovary* with 4–6 ovules; densely pubescent. *Pods* laterally compressed; densely pubescent. *Seeds* uniformly brown. Figure 5.

The extremely limited geographical distribution of *X. cordifolia* is illustrated in Figure 7. It has been recorded only from the Hex River Mountains north of Worcester in the Western Cape, where it grows in rocky areas at streamsides at 1333 to 1666 m above sea level. The only known collections are in the fruiting stage.

This species is characterized by its opposite, cordate leaves.

Specimens examined. SOUTH AFRICA. Worcester: Hex River Mountains, Milner Kloof, *Esterhuysen 32556* (BOL); Moraine Kloof, *Esterhuysen 35642* (BOL).

8. Xiphotheca canescens (Thunb.) A. L. Schutte & B.-E. van Wyk, Taxon 42: 46. 1993. *Hypocalyptus canescens* Thunb., Nov. Gen. Pl. 11: 153. 1800. TYPE: South Africa. Northern Cape, "e Cap. b. Spei," *Thunberg s.n.* (lectotype, designated by Schutte & Van Wyk (1993), UPS, Herb. Thunberg No. 16339).

Priestleya schlechteri L. Bolus, Ann. Bolus Herb. 4: 125. 1928. TYPE: South Africa. Northern Cape, Calvinia division, Onder Bokkeveld, "Oorlogs-kloof," *Schlechter 10943* (lectotype, designated by Schutte & Van Wyk (1993), BOL; isolectotypes, BM, BOL, G, K, LD, S, W, Z).

Single-stemmed, tree-like shrub up to 2.5 m tall, not sprouting after fire; woody rootstock absent.

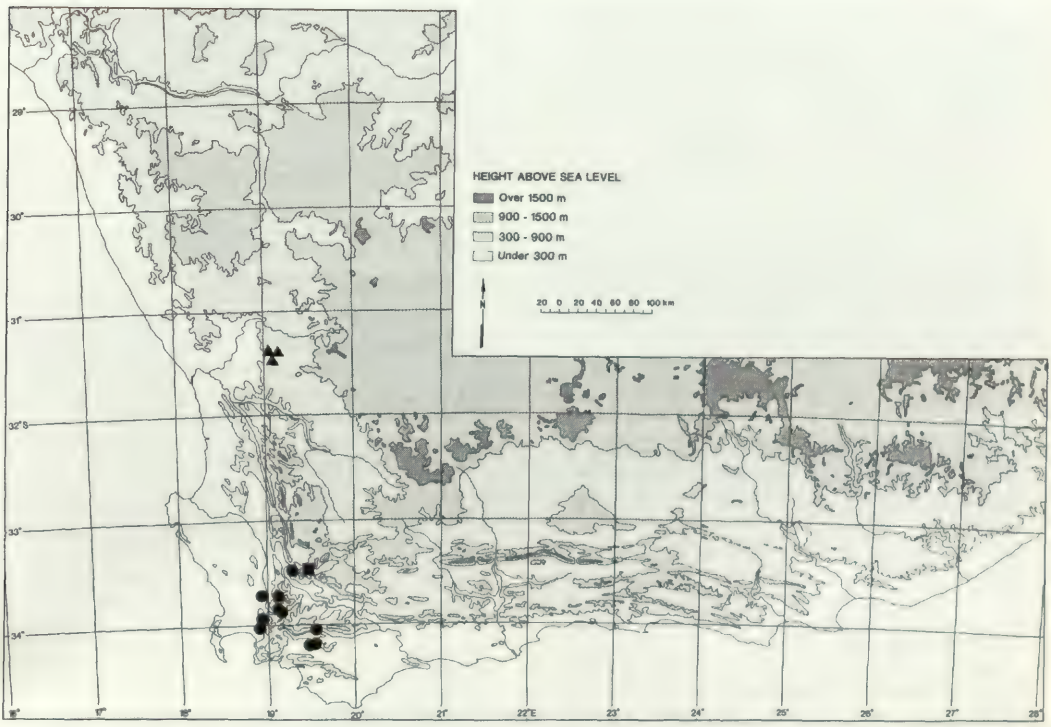

Figure 7. The known geographical distribution of *Xiphotheca canescens* (triangles), *X. elliptica* (dots), and *X. cordifolia* (square).

Leaves alternate, narrowly elliptic, flat, densely pubescent on both surfaces, glabrescent. *Inflorescences* borne at tips of lateral branches; peduncle 1.0–2.5 mm long. *Bracts* linear, ± 2 mm long. *Pedicel* 2–3 mm long. *Bracteoles* minute, caducous. *Calyx* not intrusive at base; lobes acute, shorter than the tube; carinal lobe as long as lateral lobes; densely pubescent. *Wing petals* distinctly auriculate; pocket inconspicuous on outer surface. *Ovary* with 5–8 ovules; densely pubescent. *Pods* compressed; ± glabrous. *Seeds* uniformly brown. Figure 5.

Xiphotheca canescens is a rare and highly localized species, known only from the area around Nieuwoudtville in the Northern Cape (Fig. 7). It occurs on shallow Table Mountain Sandstone in rocky areas at altitudes of 660 to 780 m.

The species is closely related to *X. elliptica*, but deviates in being a non-sprouter and having narrowly elliptic leaves with flat margins. *Xiphotheca elliptica* is a sprouter and has elliptic leaves, with slightly recurved margins.

Selected specimens examined. SOUTH AFRICA. Nieuwoudtville: Oorlogs Kloof, *Compton 20892* (NBG); top of Van Rhyns Pass, *Goldblatt 2469* (NBG); 4 mi. W of Nieuwoudtville, *Lewis s.n.* (SAM 64929); Farm Klein Arendskraal, *Van Wyk 1343* (JRAU), Farm Hotbergfontein, *Vlok & Schutte 46* (MO).

9. Xiphotheca elliptica (DC.) A. L. Schutte & B.-E. van Wyk, Taxon 42: 46. 1993. *Priestleya elliptica* DC., Prodr. 2: 122. 1825. TYPE: South Africa. Western Cape, "Cap. de B. Esp.," *Lambert s.n.* (lectotype, designated by Schutte & Van Wyk (1993), G-DC).

Ingenhoussia verticillata E. Mey., Comm. Pl. Afr. Austr. 1: 21. 1836. TYPE: South Africa. Western Cape, "Dutoitskloof, 3000–3500 ped.," *Drège s.n.* (lectotype, designated by Schutte & Van Wyk (1993), P; isolectotypes, K, S).

Many-stemmed shrub up to 1 m tall, sprouting from a woody rootstock after fire. *Leaves* subopposite, elliptic, margins slightly recurved, densely pubescent on both surfaces, glabrescent. *Inflorescences* borne at tips of lateral branches; peduncle 1.0–1.5 mm long. *Bracts* linear, 2.0–2.5 mm long. *Pedicel* 3.5–4.0 mm long. *Bracteoles* minute, caducous. *Calyx* not intrusive at base; lobes acute, shorter than the tube; carinal lobe as long as lateral lobes; densely pubescent. *Wing petals* distinctly auriculate; pocket inconspicuous on outer surface. *Ovary* with 5 or 6 ovules; densely pubescent. *Pods* laterally compressed; densely pubescent. *Seeds* uniformly brown. Figure 5.

The distribution of *X. elliptica* is limited to the

mountains above Paarl, Stellenbosch, and Caledon (Fig. 7). It grows on granite soil with an overlay of Table Mountain Sandstone at altitudes ranging between 365 and 1400 m.

See discussion under *X. canescens.*

Selected specimens examined. SOUTH AFRICA. Caledon: roadside between Caledon and Rivier Sonder End, *Cloete s.n.* (SAM 60986). Stellenbosch: Banhoek, *Lamb 3311* (SAM). Stellenbosch: Helderberg, *Parker 3742* (NBG). Caledon: Genadendal, Baviaansberg Mountain, *Prior s.n.* (SAM 15185). Paarl: Wemmershoek Mountains, Tierkloof, *Wasserfall 510* (NBG).

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A REVIEW OF THE GENUS *ECCREMOCARPUS* (BIGNONIACEAE)[1,2]

William G. D'Arcy[3]

Gentry Invitation Series

This is the first of a series of publications paying tribute to or using data left by the late Alwyn H. Gentry, who died in an airplane crash in Ecuador on August 3, 1993. The Bignoniaceae had been his primary monographic theme. From a base at the Missouri Botanical Garden, Gentry traveled to many parts of the world conducting field and herbarium studies of this family. Some of his best known taxonomic work appeared in the *Flora Neotropica* series and in the floras of Panama, Veracruz, Ecuador, and Venezuela. A summary of his life and scientific contributions, with a complete list of his publications, was provided by James S. Miller and collaborators in the *Annals of the Missouri Botanical Garden* volume 83, number 4.

Among materials left by Gentry is a computer database with information from some 55,000 collections he had examined from more than 122 herbaria around the world. He also left a series of unpublished manuscripts, including a treatment of the Bignoniaceae of Colombia, which is to be published in the *Flora de Colombia* series.

Others are encouraged to explore and utilize the rich legacy left by Al Gentry. This Invitation Series is being established for taxonomic publications by people who are relying on material left by Gentry, or who wish to pay tribute to other contributions he made to their work. Those interested should contact William G. D'Arcy at the Missouri Botanical Garden for details.—WGD

Abstract

Eccremocarpus is a genus of three species that grow in the uplands of Andean South America. The plants are vines with showy flowers. Morphology divides the genus into two groups that are also geographically separated: section *Eccremocarpus* and section *Calampelis*. This paper reviews the work left by the late Alwyn H. Gentry and that of others and reduces the number of species from former concepts to three. A key to the species and a map of their distribution are provided.

The genus *Eccremocarpus* is distinct from other Bignoniaceae in its dissected leaves, parietal placentation, and aseptate, dehiscent capsules, and it forms its own tribe, the Eccremocarpeae. It is also distinct in its elevational range, which is well above that of the rest of the family. *Eccremocarpus* includes three species forming two distinctive species groups. One of these, section *Eccremocarpus*, occurs in Colombia, Ecuador, and Peru. It includes plants of variable appearance but only two clearly distinguishable species, *Eccremocarpus huainaccapac* and *E. viridis*. The other, section *Calampelis*, with one species, *E. scaber*, occurs in Chile and Argentina and its plants show less variability.

History

Eccremocarpus was first described in 1794 by Ruiz and Pavón, who soon after (1798) described two species, *Eccremocarpus viridis* from Peru, and *E. scaber* from Chile. *Eccremocarpus scaber* was recognized in 1819 by D. Don as a separate genus, *Calampelis*, which effectively lectotypified *Eccremocarpus* with *E. viridis*. The first description and figure of *Eccremocarpus* by Ruiz and Pavón is of *E. viridis* and not of *E. scaber*. Other species described by subsequent botanists, some in other genera, are dealt with below.

Macbride (1961) treated the genus in the *Flora of Peru*, recognizing three species.

Eccremocarpus was revised by Sandwith (1965), who hesitantly recognized six species and placed them into two sections, sect. *Eccremocarpus* with five species, and sect. *Calampelis* with only *E. scaber*. Sandwith provided a description only for his new *E. vargasianus*.

[1] This paper is number 1 of the GENTRY INVITATION SERIES, in acknowledgment of contributions to the study of the Bignoniaceae made by Alwyn H. Gentry.

[2] Financial support from The John D. and Catherine T. MacArthur Foundation and the National Science Foundation (grant DEB-9509270) is acknowledged. The Field Museum of Natural History, the Royal Botanic Gardens, Kew, and The New York Botanical Garden graciously made their collections of *Eccremocarpus* available for this study.

[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

Muñoz (1966) provided a description and illustration of the Chilean *Eccremocarpus scaber*, reducing the variety *sepium* to synonymy.

The late Alwyn H. Gentry, whose aborted monographic studies of the Bignoniaceae this paper commemorates, followed the taxonomy of Sandwith. In publication, Gentry treated one species, *Eccremocarpus longiflorus*, in his floras of Ecuador (1977) and Colombia (in press), and he listed *E. huainaccapac*, *E. longiflorus*, *E. scaber*, *E. vargasianus*, and *E. viridis* for Peru (Brako & Zarucchi, 1993). These species also appear as determinations in his computerized database. However, Gentry made no reference to one species recognized by Sandwith, *E. lobbianus* Zahlbr. This element is known by scant material in Europe, and it may not have been studied by Gentry. Gentry provided a description only for *E. viridis* (as *E. longiflorus*, see Gentry 1977).

Careful review of most of the material seen by Sandwith and Gentry, and some additional collections not seen by them, has led me to the hesitant conclusion that *Eccremocarpus lobbianus*, *E. longiflorus*, *E. vargasianus*, and *E. viridis* are variants within a single species that should be known as *E. viridis*. It cannot be known whether Gentry might have continued to follow Sandwith's concepts had he lived to revise the genus as a whole, but in other treatments, he did tend to have a narrower species concept than the present author. Unfortunately, none of the students of the genus as a whole, Sandwith, Gentry, and the present writer, collected or is known to have seen wild populations of *Eccremocarpus*, although Sandwith may well have seen cultivated plants at Kew. This treatment departs from the Sandwith/Gentry concept in recognizing only three species, but in deference to the previous tradition, indication is made of how taxa and collections were viewed by these earlier workers. In citations that follow, reviewers of specimens are indicated by superscripts as: [S] N. Y. Sandwith, [G] A. H. Gentry, [!] present author. No symbol means not seen by any of these.

Systematics

The tribe Eccremocarpeae was established by A. De Candolle (1845) to embrace the single genus *Eccremocarpus*. This concept has been followed by later workers (Sandwith, 1965; Gentry & Tomb, 1979 [1980]).

Tribe Eccremocarpeae is characterized as having a 1-locular ovary with two bifid, parietal placentas (Gandhi & Thomas, 1983), a loculicidal capsule that remains fused apically, and winged seeds. The plants are vines with opposite, dissected leaves and tendrils (Melchior, 1964: 456). Gentry and Tomb (1979 [1980]) reported similarities in the pollen of *Eccremocarpus* to that of *Jacaranda* of tribe Tecomeae and to that of *Tourettia* of tribe Tourrettieae. The fruit in tribe Tecomeae also is loculicidal.

Two groups are clearly identifiable in the genus. Section *Calampelis* comprises the small-flowered, relatively uniform *Eccremocarpus scaber*, which is represented by abundant collections mainly from Chile. Section *Eccremocarpus* comprises plants similar to the type species, displaying larger flowers and fruits than in section *Calampelis*. These plants are found to the north of Chile in Peru, Ecuador, and Colombia, and they are known by fewer, more variable collections. Main differences between the two groups are given in the key to species.

The reduction of section *Eccremocarpus* into two species is done with some hesitation, especially as it breaks with the Sandwith/Gentry tradition of recognizing four or five species. Judging from the few color photographs seen, different morphs of *E. viridis* look very different, an impression stemming mainly from striking color differences in the calyces and differences in flower dimensions. Corolla length appears to differ considerably within the same inflorescence. The varying flower colors reported in cultivated plants of *E. scaber* invite suspicion that colors are variable in the northern species, too. Separating characters noted in Sandwith's key, such as pubescence and flower length, display continuous or overlapping patterns.

Eccremocarpus huainaccapac is closely related to *E. viridis* and shares many characters with it, but it is distinguished by its dense, glaucous-drying overall pubescence and its slightly larger leaflets. A much weaker case might also be made for recognizing *Eccremocarpus vargasianus*, but the evidence seen does not commend this view.

Geography

Eccremocarpus is found in the Andes of South America. Northern collections from Colombia, Ecuador, and Peru (*E. viridis*, *E. huainaccapac*) occur mainly between elevations of 3200 and 3700 m, and southern collections from Chile and southern Argentina (*E. scaber*) occur mainly from 1000 to 1800 m. This distribution is shown in the map of Figure 1. To judge by collections seen, populations are widely scattered and morphologically variable. Similar patterns occur in many other wind-dispersed groups in Andean uplands, for example, *Mnioides* (Asteraceae), *Niphogeton* (Apiaceae), *Puya* (Bromeliaceae), and *Polylepis* (Rosaceae).

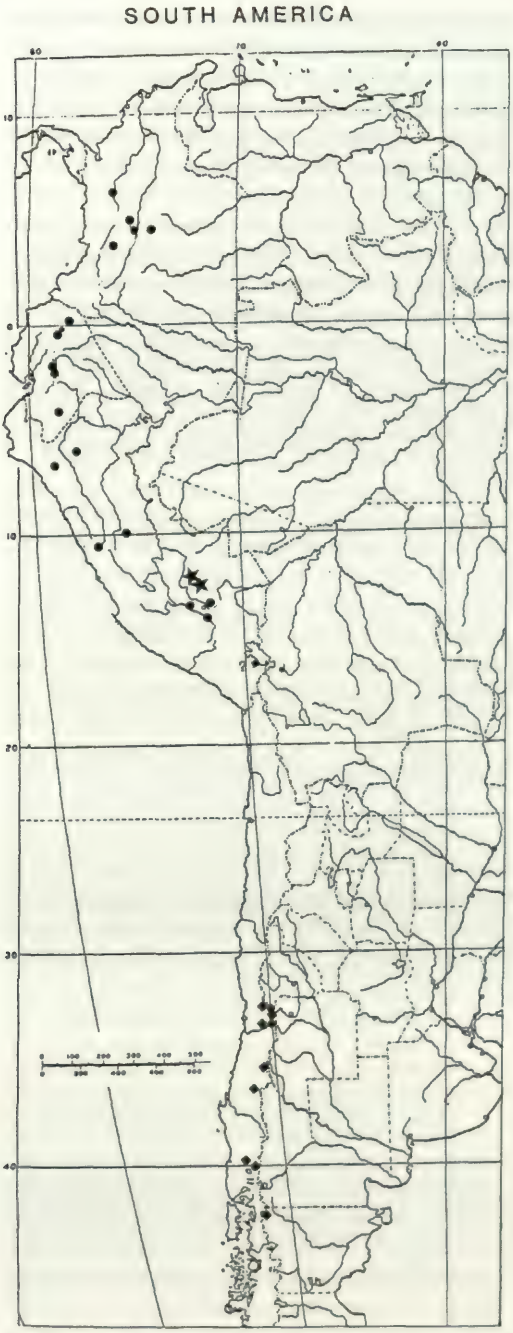

Figure 1. Map of western South America showing distribution of *Eccremocarpus* species. Diamonds = *Eccremocarpus scaber*. Stars = *Eccremocarpus huainaccapac*. Circles = *Eccremocarpus viridis*. The collection of *E. scaber* indicated in Peru is dubiously from a wild plant.

"We may generalize that wide-ranging species are the rule rather than the exception for much of the neotropical flora, especially in wind-dispersed groups" (Gentry, 1979: 342).

Taxonomic Treatment

Eccremocarpus Ruiz & Pavón, Prodr. Fl. Peruv. Chil. 90. 1794. TYPE: *Eccremocarpus viridis* Ruiz & Pavón.

Calampelis D. Don, Edinb. Phil. Jour. 7: 89. 1829. TYPE: *Calampelis scaber* (Ruiz & Pavón) Sweet = *Eccremocarpus scaber* Ruiz & Pavón.

Vines, subfrutescent, stems without anomalous vasculature, ridged and sulcate on drying, without pseudostipules or interpetiolar glands. *Leaves* opposite, bipinnatisect or tripinnatisect, a much branched tendril terminal on the leaf. *Inflorescences* racemose, generally reduced to a few flowers. *Flowers* with the *calyx* showy, often red or pink, campanulate with 5 sutures reaching near the middle, glabrous or puberulent; *corolla* showy, tubular, slightly curved or ventricose, sometimes contracted apically and almost urceolate, the lobes small, glabrous to pilose outside; *anthers* slightly exserted or situated just below the mouth of the tube, the anther medifixed and the thecae parallel or fixed near the apex and divergent; *ovary* ovoid or conical, unilocular, the ovules multiseriate on two parietal placentas; disc annular-pulvinate. *Fruit* an ovoid to ovoid-ellipsoidal capsule, the calyx persistent, unilocular, with two narrow valves that remain connected; seeds plane, suborbicular, the narrow membranous wings circling the body of the seed.

Etymology. Greek *ekkremes* = pendulous, and *karpos* = fruit.

Key to Species

1. *Flowers* less than 3 cm long; *calyx* less than 15 mm long; *fruit* evidently stipitate; *stems* glabrate; pubescence mostly glandular, hairs mostly less than 1 mm long; *leaves* often appearing alternate; leaflets petiolulate, dentate with one principal and two flanking nerves arising from near the base; plants from Chile, rare or not in Peru. Section *Calampelis* ..... 3. *E. scaber*

1'. *Flowers* mostly more than 3 cm long; *calyx* more than 15 mm long; *fruit* base hidden in the calyx; leafy part of *stems* pilose; pubescence mostly eglandular, hairs to 4 mm long; *leaves* opposite; leaflets mostly sessile or held close to the rachis, entire or grossly lobed with one principal nerve from the base and 2–3 strong lateral nerves; plants from Peru, Ecuador, or Colombia. Section *Eccremocarpus*.

2. Plants tomentose; stamens five ..... 1. *E. huainaccapac*

2′. Plants glabrate; stamens four ..... 2. *E. viridis* (includes *E. lobbianus, E. longiflorus, E. vargasianus*)

Eccremocarpus sect. **Eccremocarpus**

1. Eccremocarpus huainaccapac Vargas, Bol. Soc. Peru. Bot. 1: 15. 1948. TYPE: Peru. Cuzco: Quesser-huailla, 3900–4000 m, *Vargas 3034* (holotype, CUZ; isotypes, K[S], US[SG]).

Vine, the stem with alternating ridges and canals, pilose with copious erect weak, mostly eglandular hairs of varying length to 2.5 mm. *Leaves* opposite, generally 3–6 cm long, bipinnate with opposite pinnae, each with a terminal, ternately branched tendril and usually three primary alternate pinnae, leaflets subentire or lobed to pinnatisect and appearing 3-foliolate, mostly oblique and appearing rhombic, the terminal leaflet largest, 8–12 × 3–5 mm wide, proximal leaflets often ovate or elliptical, pilose with weak simple, light colored multicellular hairs to 1 mm long, more so beneath, discolorous, dark above; petiolules 1–2 mm long, pilose; petiole 2–6 cm long, glabrate or granular-pubescent. *Inflorescences* leaf-opposed, racemose, several to many flowered, to 14 cm long, pubescent with simple gland-tipped hairs; bracteoles ca. 10 mm long, ovoid, apically obtuse; pedicels 5–15 mm long, pilose. *Flower* buds narrowly ovoid; calyx campanulate, 8–10 × 13–15 mm, 5-dentate, split ⅓–½ way down, pilose with gland-tipped hairs; corolla basally campanulate, 40–45 mm long and 2–3 mm wide within the calyx, above cylindrical, pilose overall outside, minutely pilose basally within, 7–8 mm wide at the mouth, the lobes green, obtuse, ca. 4 mm long, glabrate; stamens 5, unequal, the filaments inserted ca. 7 mm from the base, free, sparingly pubescent at point of insertion, the anthers unequal, 5–10 mm long (in the same flower), dorsifixed near or above the middle, thecae separate but parallel below the insertion point; style exserted ca. 4 mm, the lower stigma lobe reflexed, ovary sessile, ovoid, with two pronounced longitudinal ridges, 4 mm long, the surface granular; disc annular-pulvinate with a few minute distal trichomes, ca 1.5 mm tall, ca. 6 mm wide. *Fruit* not known. Figure: Vargas (1948: 15, 16).

In the one flower examined (*Nuñez & Galiano 13414*), the shorter stamens may lack pollen. The stamens were unequal in size, and the corolla was exserted from the calyx by only 1.5 cm, suggesting that the flower was not yet fully expanded into anthesis.

Vargas (1946: 47) listed the species in *Diez Años al Servicio de la Botánica en la Universidad del Cuzco*, but did not provide a description, and the name was not validly published until 1948. In the 1946 publication, Vargas gave the type locality as Qquesser-huailla, Ckoricocha, but the specimen at US reads Igneser-Huailla.

Eccremocarpus huainaccapac is similar in form to *E. viridis*, but its overall pubescence is strikingly distinct. The name of this species honors the last Inca king, Huainacapacc (sic). Vargas (1948) supplied the common name "Chucchucha."

Distribution. This species is known from Peru, in the vicinity of Cuzco and Apurimac between 3100 and 4100 m elevation. It has been collected in flower in December and August, and the fruit is unknown.

All known specimens (*E. huainaccapac*). PERU. **Cuzco:** Qquesser-huailla, Ckoricocha, N Cuzco, 24 Dec. 1942 (fl), *Vargas 3034* (K[st], US[GS], CUZ); Urubamba, Kello Cocha, Yanacocha, 13°15′S, 72°16′W, 4150 m, (fl), *Nuñez & Galiano 13414* (MO[G]). **Apurimac:** Grau Province, Interandean valley of Coyllurqui, 13°50′S, 72°25′W, 3165 m, 26 Aug. 1991 (sterile), *Nuñez* et al. *14135* (MO[G]); Aymaraes, 160 km from Challhuanca towards Puquio, dist. Cotarosi, 4050 m, 7 Jan. 1962, *Saunders 776* (K[GS]).

2. Eccremocarpus viridis Ruiz & Pavón, Syst. Veg. Fl. Peruv. Chil. 157. 1798. TYPE: Peru. Near Muña, *Ruiz s.n.* (holotype, MA-2[S] = photo, F-29234, F-fragment).

Eccremocarpus longiflorus Humboldt & Bonpland, Pl. Aequin. 1: 229. 1808. TYPE: Ecuador. Loja: *Humboldt & Bonpland s.n.* (holotype, P = photo, F-39401).

Eccremocarpus lobbianus Zahlbr., Ann. Nat. Hofmus. Wien, 12: 103. 1897. TYPE: Peru ("Bolivia"), *Lobb s.n.* (holotype, W[S] fide Sandwith, 1965: 148), *Lobb 391* (isotype, K[st]). PARATYPE: *Maclean s.n.* (K[st]).

Eccremocarpus mutisiana Cuatrecasas, Trab. Mus. Nac. Cienc. Nat. (Madrid), ser. Bot. 26: 15, f. 9. 1933. TYPE: Colombia. Tolima: *Cuatrecasas 2743* (holotype, F[v], isotypes, K[v]).

Eccremocarpus vargasianus Sandwith, Kew Bull. 19: 406. 1965. Based on *E. viridis* sensu Vargas, Bol. Soc. Peru. 1: 15. 1948, non Ruiz & Pavón. TYPE: Peru. Cuzco: *Vargas 5956* (CUZ?, K, isotypes MO-2[G]).

Vine climbing and twining, 2–4 m long, semiwoody, the stem with alternating ridges and canals, glabrate with sparse inconspicuous ascending eglandular hairs, erect gland-tipped hairs and reduced hairs present on emerging growth, sometimes persistent at the nodes. *Leaves* opposite (sometimes one reduced or suppressed), generally 3–6 cm long, bipinnate with opposite pinnae, each with a terminal, mostly 3 times branched, wiry tendril, usually with four primary alternate pinnae, leaflets ovate or elliptical to cordate or rhomboid, 3–7(–9) mm long, 1.5–25 mm wide, glabrate to short-glan-

dular-pilose; petiolules 2–5 mm long, often pubescent; petiole 2–6 cm long, or glabrate or granular-pubescent. *Inflorescences* opposite the leaves, racemose, several flowered, to 16 cm long, pubescent with short, simple, erect, gland-tipped hairs; bracteoles 4–10 mm long, deltoid to linear, apically acute; pedicels 5–15 mm long, the flowers twisting to one side. *Flowers* with the calyx red or pink, campanulate, 8–10 × 13–30 mm, 5-lobed, split ⅓–½ way down, glabrous to pilose with simple or gland-tipped hairs, sometimes nervate, the lobes lanceolate and short-acuminate to ovate and rounded; corolla mostly yellow, green at the tip, the tube cylindrical, broader at the base, slightly curved, 3–8(–12) × 1–3 cm, slightly contracted at the mouth, ca. 4 mm wide at the mouth, glabrous or pubescent with short, erect, sometimes glandular hairs, the lobes rounded, porrect or recurved, glabrate, mostly with dense minute peltate trichomes, appearing whitish in bud; stamens four, staminode wanting, equal, inserted about 20 mm from the base of the tube, the filaments 50–55 mm long, anthers dorsifixed, inserted on the filament about halfway up, the thecae parallel, 7–10 mm long, slightly glandular pubescent; style ca. 8 cm long, the stigma situated at the corolla mouth, surrounded by the united anthers, ovary narrowly ovoid, sessile, minutely glandular papillose, 8–10 mm long, the disc annular-pulvinate, glabrous. *Fruit* ovoid or ellipsoid, 20–45 × 15–25 mm, with 4 dark grooves, dehiscing into two papery valves; the base enclosed in the calyx; fruiting calyx persistent, slightly spreading; seeds suborbicular, the body narrow, surrounded by a wing. Figures: Figure 2; Humboldt & Bonpland (1805–1817, vol. 1, fig. 65); Gentry (1977: 71 (as *E. longiflorus*)).

The characters used by Macbride (1961) and Sandwith (1965) to separate elements of this species into distinct taxa, corolla length and pubescence, are not diagnostic. There is great variation in dimensions and general appearance of flowers of this species, but the variation in most characters appears to be continuous, leading to the conclusion that a series of widely separated populations represent conspicuous variants of a single polymorphic species. Perhaps most conspicuous is corolla size and width in relation to calyx length. In some specimens (*Prieto P-151, Davies 220*), the corolla (10 cm long) greatly exceeds the calyx and is narrowly tubular throughout. Such a flower was illustrated as the type of *Eccremocarpus longiflorus*. In other cases, such as the flower illustrated as the type of *E. viridis*, the corolla is relatively broader, hardly or not exserted from the calyx. On one collection (*Davis 220*), two flowers have long (9–11 cm) corollas and two have short (6 cm), barely exserted ones. Exsertion of the stamens is also variable; some collections (*McPherson 13159*) have the stamens included in the corolla mouth and in others (*Vargas 5956*) they are clearly exserted. Stamens are subequal in length. In *Vargas 5956*, the type of *E. vargasianus*, the longer pair of stamens is only about 1 mm higher than the shorter ones. In this specimen, the corolla is narrowest below the middle. In other collections, the corolla is narrowest above, near, or below the middle, and in some collections, it is evenly cylindrical, either straight or curved, for its entire length.

A difficulty in interpreting the significance of flower features in herbarium collections is the likelihood that collections were made at different stages of flower opening, as noted under *E. huainaccapac* above and by Sandwith (1965: 147). The material underlying *E. lobbianus* and the original illustration of *E. viridis* may represent young flowers and not the dimensions and shapes of flowers when they are fully unfolded. The type material of *Eccremocarpus viridis* at Madrid and Chicago lacks flowers (Sandwith, 1965) and an indication as to where it was collected. The species concept of Sandwith was therefore shaped largely by the two other collections he cited, which are thought to come from Muña in the Huanaco Department of Peru. Thus, if *Eccremocarpus viridis* were to be divided into two or more species, it is not clear what the separated elements should be called.

Distribution. This species is found in Colombia, Ecuador, and Peru mainly between 2700 and 3600 m elevation. Most Colombian collections are from the Cordillera Central. Collections from the northern part of the range, Colombia and Ecuador and northern Peru, are much more uniform in character than those from parts of Peru from where most synonyms were described.

This species appears to flower and fruit throughout the year.

Representative specimens (Eccremocarpus viridis). COLOMBIA. **Caldas:** Nevado Del Ruiz, Carr. Termales-Refugio, 3825 m, 19 Mar. 1972, *Cleef & Hart 2500* (MO[C], U[C]); Tolima Las Mesetas, E slope of Mt. Tolima, 3600 m, 13 May 1932, *Cuatrecasas 2743* (COL[C], K[SC]). ECUADOR. **Napo:** 3200 m, 1977, *de Vries s.n.* (AAU[C]). PERU. **Cuzco:** Urubamba, Penas a Kosniriti, 3600 m, 23 Mar. 1946, *Vargas 5956* (K[SC], MO[C]).

Eccremocarpus sect. **Calampelis** (D. Don) A. DC., Prodr. 9: 238. 1845. *Calampelis* D. Don, Edinb. Phil. Jour. 7: 89. 1829. TYPE: *Calampelis scaber* (Ruiz & Pavón) Sweet = *Eccremocarpus scaber* Ruiz & Pavón.

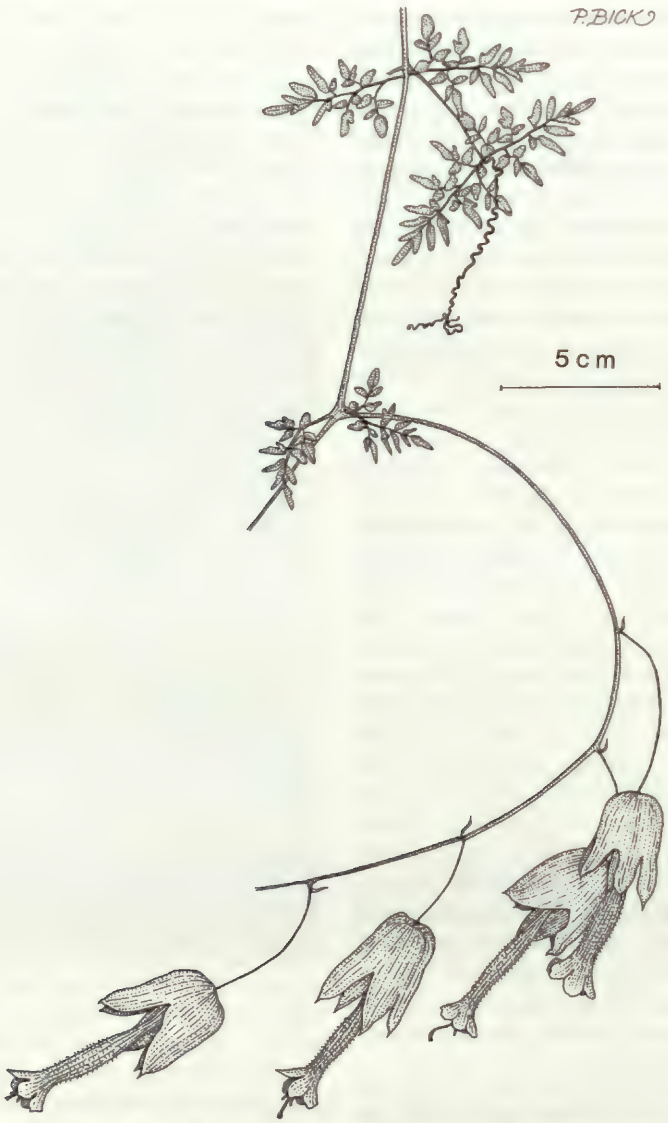

Figure 2. *Eccremocarpus viridis* Ruiz & Pavón. Inflorescence and leaves. After *Vargas 5956* (type collection of *E. vargasianus* Sandw.).

3. Eccremocarpus scaber Ruiz & Pavón, Syst. Veg. 157. 1798. *Calampelis scaber* (Ruiz & Pavón) Sweet, Brit. Fl. Gard. ser. 2. 1. t. 30. 1831. [As "*scabra.*"] TYPE: Chile. Provs. Colchagua, Rancagua, and San Jacob, *Ruiz & Pavón 1798,* (holotype, MA, photo, 029233, F).

Eccremocarpus sepium Bert. in "Merc. Chil. 1829" cf. Bull. Ferussac, 20. 111. 1830. *Eccremocarpus scaber* var. [b] *saepium* (Bert.) A. DC., Prod., 9: 239. 1845. TYPE: Chile. Sepibus secus, vias prope Rancagua S. Yago et Quillota, *Bertero 965* (BM^{G}, F$^{}$, FI^{S}, MICH^{G}, MO$^{}$, P^{G}). [Accepted as a synonym by Muñoz (1966).]

Eccremocarpus scaber var. *aurea* [sic] Benary, Gartenflora 22: 608. 1903. TYPE: cult. Hort. Schönbrunn (?W, not seen).

Eccremocarpus scaber var. *carmineus* [sic] Spigolatore, Bull. R. Soc. Toscana Orticultura 29(2): 339, fig. 22. 1904. TYPE: cultivated in ?France, not located.

Eccremocarpus scaber carmineus Pynaert, Rev. Hort. Belge 31: 55. 1905. TYPE: cult. Belgium, not located.

Eccremocarpus scaber var. *roseus* Huxley et al., New Roy Hort. Soc. Dict. Gard. 2: 122. 1992. TYPE: Not located.

Vine, climbing and twining, 2–6 m long, basally woody, the stem drying with alternating ridges and canals, puberulent with short, erect, often gland-tipped hairs and occasional weak hairs to 2 mm

long. Leaves opposite (sometimes one reduced or suppressed), generally 2–6 cm long, bipinnate with opposite pinnae, each with a terminal, mostly ternately-branched wiry tendril, usually with four primary mostly opposite pinnae, these with 3–5 leaflets, leaflets ovate to rhomboid, often oblique, 8–30 × 7–15 mm, basally cordate or truncate, apically obtuse, margins entire or dentate, shiny-grayish to dark green above, glabrate to pilose with short glandular hairs, mostly appearing as palmately 2–5-nervate; petiolules 2–5 mm long, often pubescent; petiole 2–6 cm long. *Inflorescences* opposite the leaves, sometimes appearing terminal, racemose, several to many flowered, to 25 cm long, pubescent with simple, mostly gland-tipped hairs; bracteoles 4–10 mm long, deltoid to linear and apically attenuate; pedicels 5–30 mm long. *Flowers* with the calyx red or orange (green), campanulate, ca. 8 × 4–8 mm, 5-dentate, unequally split ⅓–½ way down, puberulent with gland-tipped hairs; sometimes conspicuously nerved, corolla red or orange, sometimes yellowish near the tip, the tube subcylindrical, 20–25 × 2–3 mm wide at the base, expanded about ⅓ way up on one side to 5 mm across, contracted at the mouth, the lobes rounded, mostly recurved, glabrate, ca. 4 mm wide at the mouth; stamens four, unequal or (Muñoz) equal, 8 mm long, the filaments inserted about halfway up the corolla, then free or (Muñoz) united to about the middle of the thecae; anthers 2.4 mm long, the anther thecae basally divaricate or (Muñoz) parallel and united, the lobes of the stigma slightly expanded when closed (dried), slightly shorter than and surrounded by the anthers; ovary sessile, ovoid to conical, smooth except for two longitudinal ridges; disc annular-pulvinate, ca. 1 × 2.5 mm across, red (Muñoz). *Fruit* short-stipitate, ellipsoidal, 30–40 × 15–20 mm, glandular, with 4 dark grooves, dehiscing into two papery valves; fruiting calyx persistent and slightly curved away from the fruit base; fruiting peduncles 20–30 mm long; seeds 3–3.5 mm across, suborbicular, the body dark brown, ovoid, surrounded by a shiny, hyaline wing. Figures: Edward's Bot. Reg. (1825: t. 939*); Sweet, Brit. Fl. Gard. (1831: t. 30); Maund (1831*: 289*); Louden (1844: 1263*); Schumann (1894: fig. 93a, b); Benary (1903: 609); Spigolatore (1904: 340); Pynaert & Pynaert (1905: 55); Muñoz (1966*); Hay & Synge (1969: 247*); Hoffman J. (1978: 132*); Graf (1986: 184*); Tsukamoto (1988 vol. 3: 339*); Graf (1992: 270*); Huxley (1992: 1: 352); Belmonte et al. (1994). (* colored illustration.)

Two other names, *Tourretia scabra* Dombey and *Dombeya nodiflora* L'Her., were noted in the synonymy of this species by De Candolle (1845), but they were not validly published.

Distribution. Low cordillera in Chile from Aconcagua to Valdivia, mainly between 1000 and 1800 m, but ranging from 300 to 3000 m elevation. The species is also found in Chubut and Rio Negro, Argentina. Gentry's database recorded two collections, *Chavez 3467* and *Shepard 9*, from Cuzco and Puno Departments in Peru. The *Chavez* collection was labeled as a cultivated plant, and because Puno is so distant from the range of the species in central and southern Chile, the Shepard collection is also assumed to have been cultivated. *Eccremocarpus scaber* is occasionally cultivated outdoors in Europe as a curious ornamental. The species has been collected in flower in South America mainly from October to March, but plants in southern European gardens are said to bloom continuously (Spigolatore, 1904).

Plants of this species in European cultivation have displayed considerable variation of flower color, e.g., calyx green, corolla rose, dark red, scarlet to deep orange-red, orange, or golden (Loudon, 1844; Benary, 1903; Pynaert & Pynaert, 1905), although this variation has not been noted by Chilean writers (Muñoz, Hoffman, Navas). In addition to the names noted in synonymy under this species, Huxley (1992: 122) noted *Eccremocarpus* Anglia Hybrids, with flowers yellow, orange, pink, scarlet, and crimson, which are here considered to be forms of *E. scaber.*

Pollination of *Eccremocarpus scaber* is by hummingbirds as evidenced by notes on collections (*Elliott 247*) and the common name Chupa-chupa (*Behn s.n., Elliott 247, Kausel 1673*), a Spanish word for suck, as hummingbirds seem to do when their bills enter the flowers. A study of nectar and nectaries in *Eccremocarpus scaber* by Belmonte et al. (1994) noted pollination by Giant Hummingbirds (*Patagonia gigas gigas*).

The climbing ability of this species by means of tendrils with tactile responses has long been subject of study (Darwin, 1891; Junker & Reinhold, 1975; Tronchet, 1977; Junker, 1977).

Representative specimens (Eccremocarpus scaber). ARGENTINA. **Chubut:** entre El Bolsón y Lago Puelo, 42°05′S, 71°38′W?, 13 Nov., *Meyer 9422* (K[S]). CHILE. **Colchagua:** *Cuming 21* (BM[G]). **Curico:** Curico, Los Quenes (Andes de Curico), 35°01′S, 70°48′W, 1000 m, 20 Jan. 1942, *Aravena 33365* (MO[G]). **Santiago:** Tiltil, 33°55′S, 70°57′W, 840 m, 9 Nov. 1941, *Behn 21492* (K[S]). **Valdivia:** *Buchtien s.n.* (L[G]). **Valparaiso:** Quebrada Cale, 33°S, 71°W, 1 Mar. 1952, *Boelcke 6474* (F, MO[G], MO[G]). PERU. **Puno:** Lake Titicaca, 15°48′S, 69°24′W, 3125 m, 26 Nov. 1919, *Shepard 9* (NY[G]).

Rejected Names

Eccremocarpus ruber Regel, Cat. Pl. Hort. Aksakov. 51. 1860. Nomen nudum.

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List of Collections

Specimens are listed alphabetically by principal collector and number, followed by herbarium acronym. Identifications are indicated by numbers: **1**, *Eccremocarpus huainaccapac*; **2**, *E. viridis*; **3**, *E. scaber.* Differing identifications made by previous workers follow in parentheses: the species epithet and the workers' initials: **G:** A. H. Gentry, **S:** N. S. Sandwith.

Without collector, number (F^{I}) **3**. Without collector, number (MO^{I}) **3** EUROPE. Without collector, number (NY^{I}) **3**.

Anderson s.n. (MO^{I}) **3** EUROPE. **England.** *Aravena 33316* (MO^{GI}) **3** CHILE. **Curico.** *Aravena 33365* (MO^{GI}) **3** CHILE. **Curico.** *Ball s.n.* (NY^{GI}) **3** CHILE. **Santiago.** *Behn s.n.* (F^{I}) **3** CHILE. *Behn 21492* (K^{I}) **3** CHILE. **Santiago.** *Bertero s.n.* (NY^{GI}, P^{G}) **3** CHILE. *Bertero 231* (P^{G}) **3** CHILE. *Bertero 239* (FI^{S}) **3** CHILE. **Valparaiso.** *Bertero 965* (BM^{G}, $MICH^{G}$, MO^{I}, P^{G}) **3** CHILE. **Valparaiso.** *Bocher et al. 598* (C^{G}) **3** CHILE. **Santiago.** *Boelcke 6474* (F^{I}, MO^{GI}) **3** CHILE. **Valparaiso.** *Bridges 177* (K^{I}, P^{G}) **3** CHILE. *Buchtien s.n.* (L^{G}) **3** CHILE. **Valdivia.**

Calvert s.n. (BM^{GI}) **3** CHILE. **Valparaiso.** *Canby s.n.* (NY^{GI}) **3** CHILE. *Chavez 3467* (MO^{GI}) **3** PERU. **Cuzco.** *Cleef & Hart 2500* (MO^{GI}, U^{G}) **2** (longiflorus-G) COLOMBIA. **Caldas.** *Comber 1011* (K^{I}) **3** CHILE. *Cook & Gilbert 1237* (US?) **2** (longiflorus-MacBride) PERU. **Cuzco.** *Contreras? & Veitch 218* (K^{SG}) **2** PERU. *Crovetto 3276* (F^{I}) **3** ARGENTINA. **Chubut.** *Cuatrecasas 2743* (COL^{G}, K^{SG}) **2** (mutisianus-G,S) COLOMBIA. **Tolima.** *Cuatrecasas 9330* (COL^{G}, F-3^{I}) **2** (longiflorus-G) COLOMBIA. **Caldas.** *Cuatrecasas 9351B* (COL^{G}) **2** (longiflorus-G) COLOMBIA. **Caldas.** *Cuatrecasas 20400* (F-3^{I}) 2 COLOMBIA. **Valle.** *Cuming 21* (BM^{G}) **3** CHILE. **Colchagua.** *Cuming 615* (K^{I}) **3** CHILE. **Valparaiso.**

Davis (Davies) s.n. (MO^{GI},BM^{SG}) **2** PERU. **Huánuco.** *Davis comm. Veitch 220* (K^{SI}) **2** PERU. **Huánuco.** *Dawe* 860 (K^{S}, NY^{GI}) **2** (longiflorus-G,S) COLOMBIA. *De Barba 487* (F^{I}) **3** ARGENTINA. **Chubut.** *Devia & Prado 1880*

(MO[cf] ex TULV) **2** (longiflorus-G) COLOMBIA. **Valle.** *de Vries s.n.* (AAU[c]) **2** (longiflorus-G) ECUADOR. **Napo.** *Dombey s.n.* (P[c]) **3** CHILE. **Santiago.**

Ellenberg 4867 (MO[cf]) **2** (vargasianus-[?]) PERU. *Elliott 419* (BM[c]) **3** CHILE. *Elliott 247* (K[!]) **3** CHILE. *Elwes s.n.* (K[!]) **3** CHILE.

Fournier s.n. (P[sc]) **2** (longiflorus-G,S) ECUADOR. **Pichincha.** *Frbr. Bert. Jime. ? s.n.* (MO[cf]) **3** CHILE. *Freire et al. 656* (QCA[c]) **2** (longiflorus-G) ECUADOR. **Chimborazo.** *Frödin s.n.* (NY[cf]) **3** CHILE. **Santiago.** *Frödin 635* (BM[c]) **3** CHILE. **Aconcagua.**

Gay s.n. (K[s]) **2** (longiflorus-S) ECUADOR. *Gay s.n.* (P[c]) **3** CHILE. **Santiago.** *Gay s.n.* (P[c]) **3** CHILE. **Valdivia.** *Gay 20* (P[c]) **3** CHILE. **Santiago.** *Goodspeed 16853* (MO[!]) **3** CHILE. **Aconcagua.** *Goodspeed 23344* (K[!]) **3** CHILE. **Aconcagua.**

Halpin s.n. (CLEMS[c], K[c]) **3** CHILE. *Hartweg 148* (K[!]) **2** (longiflorus-G,S) ECUADOR. **Loja.** *Harvey s.n.* (K[st]) **3** CHILE. *Hastings 171* (NY[cf]) **3** CHILE. *Hirsch P1022* (K[!]) **2** (vargasianus-S) PERU. **Urubamba.** *Hort. Vilmourin s.n.* year 1857 (MO[!]) **3** EUROPE. **France.** *Humboldt s.n.* (K[s], MO[!], P[sc]) **2** (longiflorus-G,S) PERU. **Loja.**

Jameson s.n. (K[sc]) **2** (longiflorus-S) ECUADOR. **Pichincha.** *Jameson 56* (NY[cf]) **2** (longiflorus-G) ECUADOR. **Pichincha.** *Jameson 186* (K[sc!]) **2** (longiflorus-S) ECUADOR. **Pichincha.** *Jameson 286* (BM[sc], F[c], K, NY[c], P[sc]) **2** (longiflorus-G,S) ECUADOR. **Pichincha.**

Karsten s.n. (W[s]) **2** (longiflorus-S) COLOMBIA. **Pichincha.** *Karsten s.n.* (W[s]) **2** (longiflorus-S) ECUADOR. **Cundinamarca.** *Kausel 1673* (F[!]) **3** CHILE. **Santiago.** *King 589* (BM[c]) **3** CHILE. *King 712* (BM[c]) **3** CHILE. *Kuntze s.n.* (NY[cf]) **3** CHILE.

Leeds s.n. (F[!]) **3** U.S.A. **California.** *Lehmann 3149* (BM[sc], K[st]) **2** (longiflorus-G,S) COLOMBIA. **Caldas.** *Lobb 391* (K[st]) **2** (lobbianus-S) PERU. *Londono et al. 481* (MO[c] ex-MEDEL) **2** (longiflorus-G) COLOMBIA. **Antioquia.** *Luteyn & Tirira 1336A* (MO[!]) **2** ECUADOR. **Napo.**

Macbride 4371 (F[!], W[s]) **2** PERU. *MacLean s.n.* (K-3st) **2** (lobbianus-S) PERU. *Macrare? s.n.* (K[!]) **3** CHILE. *Mathews 3176* (BM[sc], K[!]) **2** (longiflorus-G,S) PERU. **Amazonas.** *Mathews s.n.* (BM[sc]) **2** (longiflorus-S) PERU. **Amazonas.** *Mazzei s.n.* (FI[c]) **3** CHILE. **Santiago.** *McPherson 13159* (MO[cf]) **2** (longiflorus-G) COLOMBIA. **Antioquia.** *Menzies 91* (MO[cf]) **3** CHILE. *Mexia 7887* (BM[c], F[!], MO[cf], NY[cf]) **3** CHILE. **Curico.** *Meyen s.n.* (P[c]) **3** CHILE. *Meyer 9422* (K[st]) **3** ARGENTINA. **Chubut.** *Middleton s.n.* (BM[c]) **3** CHILE. *Molau & Ohman 1635* (GB[c] = photocopy MO[!]) **2** (vargasianus-G) PERU. **Cuzco.** *Montero 67a* (MO[cf]) **3** CHILE. **Colchagua.** *Montero 260* (K[!]) **3** CHILE. **Santiago.** *Montero 507* (MO[cf]) **3** CHILE. **Santiago.** *Morrison 16853* (MO[cf]) **3** CHILE. **Aconcagua.**

Nuñez & Galiano 13414 (MO[!]) **1** PERU. **Cuzco.** *Nuñez & Luna 8841* (F[!], MO[c]) **2** (vargasianus-G!) PERU. **Cuzco.** *Nuñez et al. 14135* (MO[c]) **1** PERU. **Apurimac.**

Øllgaard et al. 38199 (AAU[c]) **2** (longiflorus-G) ECUADOR. **Chimborazo.** *Øllgaard et al. 98155* (AAU[c]) **2** (longiflorus-G) ECUADOR. **Carchi.** *Ortiz s.n.* (AAU[c], QCA[c]) **2** (longiflorus-G) ECUADOR. **Imbabura.** *Ortiz 30* (AAU[c], NY!) **2** (longiflorus-G) ECUADOR.

Pearce 533 (K[st]) **2** PERU. **Huánuco.** *Pearce 823* (K[st]) **2** (vargasianus-S) PERU. *Penland & Summers 1080* (F[!]) **2** ECUADOR. **Azuay.** *Pennell 12262* (F[!], GH, NY[cf]) **3** CHILE. **O'Higgins.** *Philippi s.n.* (HB[c]) **3** CHILE. **Santiago.** *Poeppig 2* (BM[c]) **3** CHILE. *Prance 26595* (US[c]) **2** (longiflorus-G) ECUADOR. **Napo.** *Prieto P-151* (NY[cf]= MO, photocopy) **2** (longiflorus-G,Wurdack) ECUADOR. **Cañar.** *Purdie s.n.* (P[sc], K-2st) **2** (longiflorus-G,S) COLOMBIA. **Risaralda.**

Rauh & Hirsch P.1022 (K[s]) **2** (vargasianus-S) PERU. **Urubamba.** *Raddin s.n.* (F[!]) **3** CHILE. **Santiago.** *Reed s.n.* (K[!]) **3** CHILE. **Maule.** *Rossiter 398253* (MO[!]) **3** NEW ZEALAND. *Ruiz & Pavón 5/14* (MA-3[s], BM) **2** PERU. *Ruiz & Pavón s.n.* (BM[s], F[!] ex MA, FI[s]) **3** CHILE. **Santiago.**

Sanderness 288 (K[!]) **3** CHILE. *Saunders 776* (K[st]) **1** PERU. **Apurimac.** *Schlatzer s.n.* (AAU[c]) **3** CHILE. **Santiago.** *Schmidt s.n.* (HB[c]) **3** CHILE. *Shepard 9* (NY[cf]) **3** PERU. **Puno.** *Simpson s.n.* (P[c]) **3** CHILE. *Sodiro s.n.* (P[sc]) **2** (longiflorus-G,S) COLOMBIA. **Cundinamarca.**

Triana s.n. (P[sc], COL[c]) **2** (longiflorus-G,S) COLOMBIA. **Antioquia.** *Triana 223* (P[sc]) **2** (longiflorus-G,S) COLOMBIA. **Risaralda.** *Triana 4107* (?5107,?8107,?4107) (COL[c], P[sc]) **2** (longiflorus-G,S) COLOMBIA. **Cundinamarca.**

Vargas 3034 (K[s], US[sc]) **1** PERU. **Cuzco.** *Vargas 5956* (K[st], MO[cf]) **2** (vargasianus-G,S) PERU. **Cuzco.** *Vargas 20079* (MO[cf]) **2** (vargasianus-G) PERU. **Cuzco.** *Vargas 22644* (MO[cf]) **2** (vargasianus-G) PERU. **Cuzco.** *Vieillard 84* (P[c]) **3** CHILE. **Valparaiso.**

Weberbauer (F?) **2** (longiflorus-Macbride, S) PERU. **Cajamarca.** *Weberbauer* 4938 (?) **2** (longiflorus-Macbride,S) ECUADOR. *Werdermann 482* (BM[c], F[!], HB[c], MO[cf], U[c]) **3** CHILE. **Santiago.** *Wildenow s.n.* (HB[c]) **3** CHILE.

Zöllner 6486 (L[c]) **3** CHILE. **Aconcagua.** *Zöllner 9350* (MO[cf]) **3** CHILE. **Valparaiso.** *Zöllner 11052* (MO[cf]) **3** CHILE. **Santiago.**

Index

Calampelis 105, 107, 108
scaber 105, 107
scabra 108
Dombeya
nodiflora 109
Eccremocarpus 105, 106
huainaccapac 106
lobbianus 106
mutisiana 106
scaber 105, 107, 108
scaber carmineus 108
scaber var. *aurea* 108
scaber var. *carmineus* 108
scaber var. *roseus* 108
scaber var. [b] *saepium* 108
sepium 108
vargasianus 106
viridis 105, 106
Tourretia
scabra 109

HOT-SPOTS ANALYSIS FOR CONSERVATION OF PLANT BIODIVERSITY IN THE MEDITERRANEAN BASIN[1]

Frédéric Médail[2] and Pierre Quézel[2]

Abstract

Due to the increase of human impact on the world scale, there is an urgent need to identify the sectors of the greatest biodiversity that are also the most endangered. Examination of the plant biodiversity of the five regions with a mediterranean climate (SW Australia, the Cape region of South Africa, California, mediterranean Chile, and the Mediterranean basin) clearly demonstrates their key role in the world context. The delimitation and definition of 10 red alert areas or "hot-spots" situated in the Mediterranean basin and in Macaronesia are explained in detail. The 10 sectors identified are: the Canary Islands and Madeira, the High and Middle Atlas mountains, the Baetic-Rifan complex, the Maritime and Ligurian Alps, the Tyrrhenian Islands, Southern and Central Greece, Crete, Anatolia and Cyprus, the Syria-Lebanon-Israel area and, lastly, the Cyrenaic Mediterranean. There are two main centers of biodiversity in the Mediterranean basin: one in the west that includes the Iberian Peninsula and Morocco, and one in the East that includes Turkey and Greece. This analysis demonstrates the uniqueness and fragility of the island habitats.

Résumé

L'augmentation de l'impact anthropique à l'échelle du Globe nécessite d'identifier de façon urgente les secteurs de plus haute biodiversité, qui présentent également les plus grandes menaces. L'examen de la biodiversité végétale des cinq régions soumises au bioclimat méditerranéen (S.W. de l'Australie, région du Cap en Afrique du sud, Californie, Chili méditerranéen et bassin méditerranéen) souligne nettement leur rôle clé, par rapport au contexte mondial. La délimitation et la description de 10 zones-rouges, situées dans le bassin méditerranéen et en Macaronésie, sont développées. Les 10 secteurs identifiés sont: les îles Canaries et Madère, le Haut et le Moyen Atlas, le complexe bético-rifain, les Alpes maritimes et ligures, les îles tyrrhéniennes, le sud et le centre de la Grèce, la Crète, l'Anatolie et Chypre, l'ensemble Syrie-Liban-Israël, et, enfin la Cyrénaïque méditerranéenne. Deux pôles principaux de biodiversité existent sur le pourtour méditerranéen: un occidental qui comprend la péninsule ibérique et le Maroc, et un oriental englobant la Turquie et la Grèce. L'originalité des ensembles insulaires et leur fragilité se dégagent de cette analyse.

A few years ago, addressing increasing human impact on a world scale, the scientific community sounded an alarm, pointing out the harmful effects that would result from a decrease in biodiversity (e.g., Wilson, 1988; Lubchenco et al., 1991; Solbrig, 1992; Chauvet & Olivier, 1993; Levèque, 1994). This issue reached its pinnacle with the Convention on Biological Diversity, signed during the Rio Summit in June 1992, with the adoption of Agenda 21.

The accelerated decrease in the surface area of tropical forests (e.g., Myers, 1986; Forget, 1994) monopolized attention because this biome is seen as the world's principal pole of biodiversity (Gentry, 1982, 1988). Alpha diversity thus reaches record levels in Amazonia, where, in Ecuador—in a 1-ha plot—Valencia et al. (1994) listed no less than 473 different species of phanerophytes with stems at least 5 cm in diameter, while Duivenvoorden (1994) observed 310 higher plants in a plot of 0.1 ha in Colombia.

In this context, identification of areas of major biodiversity is very desirable, considering that rates of extinction are unprecedented (Stanley, 1987). The current rate of disappearance of species is 1,000 to 10,000 times greater than that of major geological periods of mass extinction (Wilson, 1988). Myers (1988, 1990) developed an analytical methodology that enabled him to define red alert areas of biodiversity (known as "hot-spot areas"). A "hot-spot" is a sector with an exceptional concentration of species and a high rate of endemism

[1] We are grateful for helpful comments by D. Jeanmonod, P. Ponel, A. Strid, T. Tatoni, and R. Verlaque, and for suggestions from S. Pignatti concerning biodiversity areas in Italy. We also thank M. Field for linguistic advice.

[2] Université d'Aix-Marseille III, Faculté des Sciences de Marseille-St Jérôme, Institut Méditerranéen d'Ecologie et de Paléoécologie, C.N.R.S, URA 1152, Laboratoire de botanique et d'écologie méditerranéenne, Case 461, F-13397 Marseille cedex 20, France.

that is in great danger of destruction. Species richness and endemism are two attributes of biodiversity commonly used in Conservation Biology because they reflect the complexity and uniqueness of ecosystems (Caldecott et al., 1996), and also because data for them is relatively easy to obtain on a global level. By limiting himself to the plant composition, Myers (1988) first defined 10 hot-spots in tropical forests, then four others in the same biome and four in the mediterranean bioclimate (SW Australia, the Cape region of South Africa, California, and part of Chile: Myers, 1990). This author had already emphasized the important role played by the circum-Mediterranean area as a reservoir of plant biodiversity. However, he cautiously refrained from regarding the entire Mediterranean basin as a hot-spot, arguing that it covers too large an area and that there is insufficient knowledge concerning certain parts of this area. Davis et al. (1994) recently drew up a list of 250 centers of plant diversity for the entire world, but this remarkable synthesis does not give details of all the Mediterranean hot-spots.

Therefore, more detailed analyses on the scale of the Mediterranean basin are necessary in order to try to establish a comparative study of the floristic richness and endemism of the various countries around the edge of the Mediterranean. This is possible for the total number of taxa that are present, i.e., 25,000 species (Quézel, 1985) or 30,000 species and subspecies (Greuter, 1991), but also for the endemic species (around 12,500). Even if these estimates are often imprecise, they can nevertheless provide precious information on both the location of the main centers of endemism and the situation of the areas of high biodiversity. They can also give an idea of the level of threat posed to any part of the basin, particularly after the work carried out in this direction by the International Union for Conservation of Nature (I.U.C.N., 1980, 1983).

Sites and Methods

Limits of the Mediterranean Region

The question of the limits of the Mediterranean region has been approached in various ways, including from the point of view of floristic methods, the analysis of vegetation structures, climatic interpretations, and, lastly, bioclimatic criteria. Although the validity of the Mediterranean isoclimatic area (Daget, 1977) is often accepted, it seems more realistic to use more traditional boundaries. Therefore we adopted (Figs. 1, 2) the limits drawn in the Natural Vegetation Map of the Countries of the Council of Europe (Conseil de l'Europe, 1987) and in the map of the vegetation of the eastern Mediterranean (Quézel & Barbero, 1985) for the countries of the northern Mediterranean, and the 100-mm isohyet, which remains a standard for defining the southern boundary between the mediterranean bioclimate and the Sahara, even if the 150-mm value would be locally more exact nowadays (Quézel & Barbero, 1993). The defined Mediterranean region thus covers an area of around 2,300,000 km^2 (Quézel, 1985). The archipelagos of the Canaries and Madeira have also been taken into account because, from a biogeographical viewpoint, these islands are now considered as a superprovince of the Canaries subregion, which is itself incorporated in the Mediterranean region (Rivas-Martinez et al., 1993).

Estimation of the Floristic Richness and Endemism of the Mediterranean Region

One of the main difficulties in estimating Mediterranean biodiversity is that there is rarely any direct correspondence between the biogeographical boundaries and the political boundaries of a state, while the floristic assessments are nearly always prepared according to the latter criterion. However, an attempt has been made by one of us (Quézel, 1985) and these results were later accepted by several authors, including Greuter (1995) and Heywood (1995). Precise assessments for the Turkish Mediterranean region still have to be established because its separation from the Irano-Touranian area is still a matter of debate; these communities share unquestionable biogeographical and bioclimatic affinities.

The inconsistent floristic knowledge of the different countries of the Mediterranean perimeter is also an obstacle. Some sectors—Italy, Turkey, Andalusia, Crete, and Corsica—are classified according to modern floras, while others still do not have complete floras (Morocco, Spain, the Balkans, Albania). The taxonomic levels also vary greatly, according to whether taxonomists adopt a restrictive approach or take the taxonomic breakdown further than is normally accepted. In addition to the recognition and fluctuating taxonomic status of some taxa, there is the problem of whether or not to take into account highly polymorphic groups, which are often apomictic, such as *Hieracium, Taraxacum, Achillea, Rosa, Rubus,* and *Limonium.* Thus, in Sardinia, no less than 23 endemic species of *Limonium* were recently described (Arrigoni, 1976–1991), i.e., 22% of the total local endemic flora. Furthermore, some assessments made take into account only the species, while others consider the species

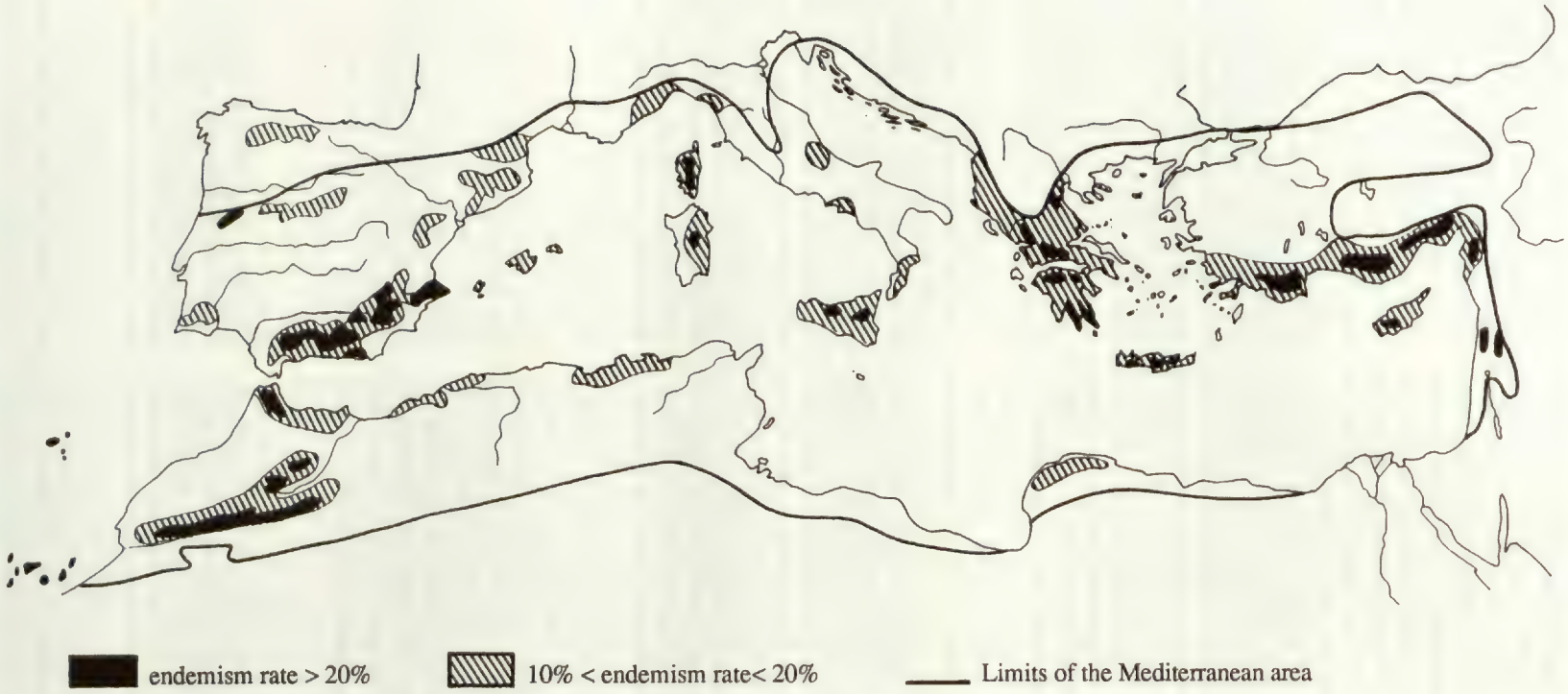

Figure 1. Biogeographical sectors with high incidences of plant endemism in Mediterranean basin.

Figure 2. Mediterranean basin hot-spots. 1: Canaries and Madeiran archipelagos. 2: High and Middle Atlas Mountains. 3: Baetic-Rifan complex. 4: Maritime and Ligurian Alps. 5: Tyrrhenian islands. 6: Southern and Central Greece. 7: Crete. 8: Anatolia and Cyprus. 9: Syria–Lebanon–Israel. 10: Mediterranean Cyrenaic. The thick line defines the limits of the Mediterranean area.

and subspecies, or even the varieties and doubtful forms, without necessarily specifying this clearly. Since it is impossible to ensure uniformity of the results, we have indicated the sources used in the published tables, on the understanding that, the estimation of the number of endemics and subendemics (endemics common to several countries, sensu Pignatti, 1982), was problematic or even impossible in some cases.

The definition and delimitation of endemic taxa are often subjective and quite difficult because authors usually characterize endemic as a species restricted to a politically defined territory without biogeographical consideration. According to Strid (pers. comm.), biogeographers ought to develop a classification of endemics reflecting real distribution area and degree of ecological specialization. Mountain endemism includes the endemic species and subspecies regularly found above an altitude of ca. 1600 m, i.e., in the Mountain-Mediterranean, Oro-Mediterranean, and Alti-Mediterranean zones.

However, the data for the Mediterranean and the Macaronesian islands are much more precise, following recent well-documented works (Shmida & Werger, 1992; Gamisans & Jeanmonod, 1993; Turland et al., 1993; Press & Short, 1994) and the results of a recent conference (held in 1993) devoted to the flora of the islands of the Mediterranean.

Results

Biodiversity of the Mediterranean Biome in the World Context

According to the recent world overview study by Davis et al. (1986) for the I.U.C.N., the five regions with a mediterranean climate (the Mediterranean basin, California, the South African Cape, SW Australia, and mediterranean Chile) have remarkable biodiversity. Table 1 shows the results reworked by Myers (1990), particularly after Goldblatt's (1978) estimates for the Cape area or those of Raven and Axelrod (1978) for mediterranean California. Floristic patterns in mediterranean-type ecosystems of southwestern Australia are still unclear: Hobbs et al. (1995) made an estimation of 8000 species in the Southwest Botanical Province, with about 75% endemism; we keep this number but we stress that it is double Myers's estimate.

Thus, the mediterranean biome, only 2% of the world's surface area, contains 20% of the total world floristic range. The estimated total number of mediterranean plants varies between 45,000 and 60,000 species (Heywood, 1995). This difference is mainly due to the inclusion of either the South African Cape (90,000 km^2) or the whole of South Africa (2,573,000 km^2). From the biogeographical viewpoint, it would be preferable to take the value of 45,000 species. Thus, South Africa, SW Australia, California, and mediterranean Chile contain 8% of the plant biodiversity in 0.3% of the earth's surface area (Myers, 1990).

Despite its considerable area, the circum-Mediterranean world is a major contributor to the biodiversity of the mediterranean biome, since 10% of the higher plants are found there in 1.6% of the earth's surface. It is interesting to compare this circum-Mediterranean biodiversity with that of other regions, both temperate and tropical. Thus, although it covers one-tenth of the area of the former U.S.S.R., the Mediterranean basin contains 4,000 more species. Similar comparisons with the United States, Europe, and China are clearly in favor of the circum-Mediterranean region. Even certain tropical or subtropical countries such as India or Zaire have less biodiversity, while Brazil has twice as many species but covers an area four times greater. Note again that the whole of tropical Africa contains only around 30,000 plant species (Good, 1974) in an area four times greater than the circum-Mediterranean region.

Calculation of the number of species per 1000 km^2 provides an evaluation that is independent of surface area. For the mediterranean biome, we obtain values of between 95.5 species for 1000 km^2 in the Cape region to 10.8 for the Mediterranean basin (Table 1). This can be compared with: 1 species/1000 km^2 in Europe, 3.1 in China, 4.7 in Zaire and in India, 6.5 in Brazil, 40 in Colombia, and 90 in Panama.

The number of endemic species in the Mediterranean region also reaches very high values, usually at least equal to those found in most tropical areas of the world. Only islands such as Borneo, Cuba, New Caledonia, Hispaniola, New Zealand (Gentry, 1986), or high-altitude habitats are richer in endemic species, but in relatively limited areas.

Biodiversity of the World's Mediterranean Climate Regions

In relation to the other mediterranean climate regions, the Mediterranean basin has the greatest variety of species, both general and endemic, but in a much greater surface area (84% of the total). Despite the considerable differences in surface area, the two mediterranean climate regions of the northern hemisphere contain a virtually equal percentage of endemic species (Table 1). Furthermore, mediterranean California has more or less the same

Table 1. Plant biodiversity of the world's five mediterranean climate regions (1: Quézel, 1985; 2: Myers, 1990; 3: Hobbs et al., 1995; 4: Bond & Goldblatt, 1984).

	Areas (km²)	Approximate number of species	Number of species per 1000 km²	Endemic species Approximate number	%
North hemisphere					
Mediterranean basin (1)	2,300,000	25,000	10.8	12,500	50
California Floristic Province (2)	324,000	4,450	13.7	2,140	48
Austral hemisphere					
Mediterranean Chile (2)	140,000	2,900	20.7	1,450	50
S.W. Australia (3)	112,260	8,000	71	6,000	75
Cape Floristic Region (South Africa) (4)	90,000	8,600	95.5	5,860	68
Total	2,966,260	48,950	16.5	27,950	57
(%/World)	(2%)	(20%)			

surface area and general biodiversity as Morocco, but California is four times richer in strictly local endemics. However, the situation is reversed if, in Morocco, we consider all circum-Mediterranean endemics in the broad sense. The case of mediterranean regions in the southern hemisphere is even more remarkable, since, due to the long geographical isolation of these areas, the endemic richness reaches up to 70% in South Africa (the Cape region) and in SW Australia. The mediterranean region of the Cape, particularly the Cape Peninsula (Cowling et al., 1996), offers an extraordinarily rich flora: around 8600 species (Goldblatt, 1978; Bond & Goldblatt, 1984), including 5860 endemics, are found there, in a surface area equal to that of Greece, which makes it one of the most remarkable hot-spots in the world.

BIODIVERSITY OF THE MEDITERRANEAN BASIN AND MACARONESIA

Despite the above-mentioned various obstacles to the establishment of an accurate assessment of circum-Mediterranean biodiversity, and with certain reservations regarding the accuracy of the values quoted, certain points can be stressed (Tables 2 and 3):

—The Mediterranean parts of Turkey and Spain are found to have the richest variety (around 5000 species), followed by Greece, Italy, France, and Morocco (with more than 3000 species).

—The percentage of endemics is highest in Turkey (31%), then Morocco (21%), Spain (19%), Greece, Syria-Lebanon, and Italy. Greece is an interesting case: endemism is indeed high, particularly in the mountains, with 27% (Strid, 1993), and it would be even higher if all the Aegean perimeter were taken as a single entity. Similarly, evaluations that take into account the Ibero-Moroccan complex would at least double the number of endemics in these sectors. Furthermore, assessment of endemics by country or by biogeographical zone never or rarely includes the endemics of the entire Mediterranean basin, which clearly underestimates the indicated rate of endemism.

—The specific nature of the islands included within the Macaronesian complex, where, for historical reasons (Suning, 1979; Bramwell, 1985; Quézel, 1995) and due to the limited amount of competition, the percentage of endemism reaches very high levels in Madeira (26%) and in the Canaries (38%), while there is a rather limited specific richness. The same situation is found, but to a lesser degree, in the islands of the Mediterranean Sea, where endemism is generally around 10% but the overall range of flora is greater, with between 1500 and 2500 taxa.

Therefore, in simplified terms, there are two major centers of biodiversity in the Mediterranean basin: a western center, including the Iberian peninsula and Morocco, and an eastern pole that encompasses Turkey and Greece. The islands of the Mediterranean Sea and, to a greater degree, the Macaronesian islands, have a very high rate of endemism.

MAXIMAL BIODIVERSITY AREAS OF THE MEDITERRANEAN BASIN AND MACARONESIA

The circum-Mediterranean region is—according to the geographical zones of which it is composed—considerably varied in both its number of species and its number of endemics. Thus we should use biogeographical concepts in order to define circum-Mediterranean hot-spots, and political boundaries should be ignored.

Initially, we attempted to determine the biogeo-

Table 2. Plant biodiversity of the countries from the Mediterranean basin (islands excluded). The figures indicate the number of species, except for the values marked with an asterisk, which also include subspecies. Unless otherwise indicated, sources are: (a): Davis et al. (1986) and (b): Quézel (1985). Other sources: (c): original observations, (d): Greuter (1991), (e): Fennane & Ibn Tattou (1995), (f): Enriquez-Barroso & Gomez-Campo (1991), (g): Bartolo et al. (1977), (h): Boulos (1995), (i): Davis et al. (1994), (j): Davis (1988), (k): I.U.C.N. (1980), (l): Olivier et al. (1995), (m): Gomez-Campo et al. (1984).

Countries	Total areas (a) (km^2)	Areas in Mediterranean bioclimate (b) (km^2)	Approximate number of species		Number and approximate % of endemic plants	
			Total (a)	In Mediterranean region (b)	Number	%
Morocco	659,900	300,000	4,200	*3,800	*900 (e)	21.4
Algeria	2,381,000	300,000	3,150	2,700	*320 (d)	10.1
Tunisia	164,000	100,000	1,800	1,600	*39 (f)	2.1
Libya	1,759,000	100,000	1,600	1,400	*140 (g)	8.7
Egypt	1,000,000	15,000	2,060	1,100	61 (h)	3
Israel	20,700	10,000	2,200	2,000	*165 (i)	7.5
Jordan	97,600	10,000	2,200	1,800 (c)	145 (i)	6.6
Syria	185,000	50,000	3,100	2,600 (c)	*395 (i)	12.7
Lebanon	10,400	10,000	2,600	2,600	311 (i)	12
Turkey	779,000	480,000	8,600	5,000	2,651 (j)	30.8
Continental Greece	107,000	90,000	5,700	*4,000	*742 (i)	13
Albania	28,700	20,000	3,000	2,200	46 (k)	1.5
Former Yugoslavia	255,000	40,000	5,000	2,500	*320 (i)	6.4
Continental Italy	251,400	200,000	4,870 (c)	3,850 (c)	570 (c)	11.7
Continental France	549,600	50,000	4,800	3,200	180 (l)	3.7
Continental Spain	504,000	400,000	6,720 (d)	5,000	1,286 (d)	19.1
Portugal	91,000	70,000	2,600 (d)	2,500	114 (m)	4.4

Table 3. Plant biodiversity of the Mediterranean and Macaronesian islands. The figures indicate the numbers of species and subspecies, except for the values marked with an asterisk, which also include varieties. Rare and threatened taxa correspond to Ex, E, V, R, I, and K categories of I.U.C.N. Sources: (a): Davis et al. (1986), (b): Gamisans & Jeanmonod (1993), (c): Bocchieri (1995), (d): Raimondo et al. (1994), (e): Lanfranco (1995), (f): Turland et al. (1993), (g): Alziar (1995), (h): Schmida & Werger (1992), (i): Dalgaard (1994), (j): I.U.C.N. (1980), (k): Original observations, (l): Médail & Verlaque (1997), (m): Polunin (1987), (n): Mus (1995, modified), (o): Verlaque pers. comm., (p): Leon et al. (1985), (q): I.U.C.N. (1983).

	Area (km^2)	Number of indigenous species and subspecies	Endemism in total flora s. str.	Endemism in total flora s.l.	% endemic species/flora		Rare and threatened taxa (endemics + non endemics)
					s. str.	s.l.	
Balearic Islands	5,014	1,450 (a)	94 (j)	180 (o)	6.5	12.4	59 (n)
Corsica	8,748	2,354 (b)	*130 (b)	270 (b)	5.5	11.5	90 (o)
Sardinia	24,090	2,054 (c)	106 (k)	200 (k)	5.2	9.7	39 (p)
Sicily	25,708	2,700 (d)	260 (o)	310 (o)	9.6	11.5	654 (d)
Malta	316	700 (e)	16 (e)	32 (k)	2.3	4.6	12 (p)
Crete (incl. Karpathos)	8,700	1,706 (f)	171 (f)	200 (m)	10	11.7	119 (q)
Cyprus	9,250	1,620 (g)	130 (g)	170 (g)	8	10.5	69 (p)
Canaries	7,273	1,582 (h)	504 (h)	600 (k)	31.8	37.9	432 (k)
Madeira Archipelago	796	670 (i)	113 (i)	175 (i)	16.9	26.1	137 (q)

graphical sectors where the rate of endemism is more than 20%; this figure is generally considered by biogeographers as delimiting a high level of endemism (Greuter, 1991; Quézel, 1995). Such percentages are not exceptional, particularly in the island and mountain areas, as demonstrated by Gomez-Campo et al. (1984) for the Iberian peninsula, where values of more than 50% are reached in the Baetican cordillera. All these zones were mentioned in Figure 1, where other areas can be distinguished, such as the Canary Islands and Madeira, the Middle and High Atlas ranges and the Rif in Morocco, the Sierra de Estrela in Portugal, as well as the upper mountain areas of Corsica, Sicily (Madonia and Etna), and probably Sardinia (Gennargentu mountain) in the central Mediterranean. Further to the east, endemism is very high in the upper mountain areas of southern Greece and of Crete, the Taurus ranges of Anatolia, the Troodos mountain of Cyprus, and the summits of the Lebanon and the Anti-Lebanon.

Other areas with a rate of endemism of around 10% deserve mention (Fig. 1): Sierra de Monchique in southern Portugal, Sierra de Gredos in the center-west of Spain, the hills of Teruel and Catalonia in the northwest, the Balearic Islands, the eastern Pyrenees, the Maritime and Ligurian Alps, the whole of Corsica and Sicily, some parts of the Italian peninsula (Pignatti, in litt. 1994), the coasts of Montenegro and Albania, the Pindus range and mount Athos peninsula in Greece, Cyprus and Crete considered together, the Mediterranean Cyrenaic, and the coastal Tell Atlas of Orania and Kabylia in Algeria.

Another way of estimating biodiversity is to identify zones of great floristic species richness, which, together with a study of endemism, would help to define hot-spots. In the present case, we selected geographical zones in their own right that cover a small or medium surface area, where the floristic variety is greater than 2000 species per 15,000 km^2. In the circum-Mediterranean region, the sectors that satisfy these criteria are certainly numerous, although they are sometimes difficult to define because of insufficient floristic knowledge for precise zones. However, the following can be included in this group: the Baetic-Rifan complex, the eastern Pyrenees, the Maritime and Ligurian Alps, Corsica and Sicily, the central Appennines and Calabria, the Dalmatian coast, Albania, Greece, Crete, the Amanus-Taurus region, the Syrian-Lebanese coast, Israel, and the coastal areas of Orania and Kabylia.

THREATS TO MEDITERRANEAN PLANT DIVERSITY

There are two very different situations in the circum-Mediterranean region relative to human impact (Barbero et al., 1990). The non-coastal zonal ecosystems of the northern part of the basin (France, Italy, and Greece) are markedly free of disturbance, and this leads to the extension of preforest and forest areas dominated by expansionist species. These include the *Pinus* species, which have remarkable ecological and biological plasticity and very high dissemination capacities (Barbero & Quézel, 1989). This extension of phanerophytes and also of chamaephytes tends to cause regression of formations of reduced vegetation cover, particularly the pastures, which are among the ecosystems that are the richest in Mediterranean taxa and in endemics. Therefore the collapse of the agro-sylvopastoral system of previous centuries causes major modifications to the structure and architecture of phytocenoses, with standardization of the flora and fauna. The Mediterranean elements tend to be replaced by medio-European species that are more ubiquitous. On the other hand, there is strong human pressure on a large part of the coastal and juxta-coastal areas, which poses a serious threat to halo-psammophile and palustral species. Island ecosystems are also very affected by the development of mass tourism.

The areas in the southern part of the Mediterranean basin (in particular North Africa) are subjected to the major impacts of the constant increases in population and in livestock, which totally destructure the ecosystems and the soils, causing strong erosive phenomena and very poor regeneration. This population explosion of the southern countries remains the major problem: their total population was 40 million in 1900, is now 290 million, and will probably reach 370 million by the year 2000 (Le Houérou, 1991).

Various recent works have tried to assess the risks incurred by the Mediterranean flora (Gomez-Campo, 1985; Quézel & Barbero, 1990; Ramade, 1990). The I.U.C.N. organization was a pioneer, and Leon et al. (1985) published a general assessment for all circum-Mediterranean flora and endemics (Table 4). Naturally, these results are open to question because they were established by various researchers who did not all have the same conception of the threats and the various categories proposed by I.U.C.N. to assess the risks. In addition, the exact situation of several species in several countries is unknown. However, according to this overview, 53% of the endemic species, i.e., 1529 taxa, are endangered (excluding Syria, Lebanon, and Turkey). One should be cautious before proposing values for the entire flora, but an analysis of the Algerian flora (Mathez et al., 1985) showed that almost 50% of the species had not been observed

Table 4. Threats affecting Mediterranean endemic plants, in countries where data are available (Leon et al., 1985, modified). Other sources: (a): Mus (1995), (b): Bramwell (1990), (c): Montmollin & Iatrou (1995), (d): Olivier et al. (1995), (e): Conti et al. (1992), (f): Raimondo et al. (1994).

Country or island	Extinct	Endangered and vulnerable	Rare or unknown
Albania	0	3	19
Algeria	1	53	80
Balearic Islands (a)	1	18	29
Canaries (b)	1	243	162
Corsica	1	32	3
Crete (c)	0	18	67
Cyprus	0	19	50
Egypt	2	18	48
France (d)	0	55	21
Greece	5	61	435
Israel	0	3	10
Italy (e)	0	98	108
Libya	0	20	42
Madeira	0	47	61
Morocco	0	4	238
Portugal	2	22	34
Sardinia	0	8	10
Sicily (f)	4	107	161
Spain	1	32	202
Tunisia	0	1	1
Former Yugoslavia	1	7	119

again for 20 years. The situation is also very worrying in Macaronesia, where more than 20% of the flora is endangered (I.U.C.N., 1983). Leon et al. (1985) listed only 16 species that have become extinct in the Mediterranean region since the beginning of the century. Recently, Greuter (1994) indicated that 37 species and subspecies of vascular plants of the Mediterranean area are presumed to be extinct. Nevertheless, these results are infinitely too optimistic to have any real significance, particularly for the countries of the southern Mediterranean. Furthermore, if we could really take into account the erosion of the different habitat types and of the number of populations of rare species, the situation would be undoubtedly worse that it seems.

Discussion

The results and analyses mentioned above can be used to identify sectors of the greatest general biodiversity with the greatest number of endemics that appear to be the most endangered, i.e., the "hot-spots" (Fig. 2) as defined by Myers (1988, 1990). We distinguished 10 sectors, which clearly fit Myers's definition, in the circum-Mediterranean region and we summarize the main threats to these hot-spots (Table 5). Some other zones (the Dalmatian coast, the eastern Pyrenees, and some parts of the Italian peninsula, or even Kabylia) could have been defined as hot-spots, but the data concerning them is too incomplete.

Archipelagos of the Canaries and Madeira

These islands of quite recent volcanic origin (5 to 7 million years: Carracedo, 1980) with a surface area of 8100 km², which are not connected to the continent, were apparently colonized by the long-distance transport of diaspora (Shmida & Werger, 1992). The initial absence of competition allowed strong adaptive radiation (Lems, 1960; Bramwell, 1975) and the establishment of a unique post-Miocene flora with a rich variety of endemics (Humphries, 1979; Bramwell, 1976, 1985; Quézel, 1995). Thus, of the total number of species 38% are endemic in the Canaries (Schmida & Werger, 1992) and 26% in Madeira (Dalgaard, 1994). But this unique flora is endangered (27% of the endemic flora in Madeira and 41% in the Canaries, according to the I.U.C.N., 1983). The Canaries archipelago is subjected to drastic human impact in its low-altitude zones by a considerable tourism infrastructure and the development of banana plantations. Infracanarian formations of cactoid *Euphorbia* and (to a greater extent) laurel woods have clearly regressed (Santos, 1990). Thus, the Gran Canaria laurisilva now covers less than 1% of its original area, while 90% of Tenerife's laurel woods have disappeared (Bramwell, 1990). Trees such as *Phoenix canariensis* Chab. and *Dracaena drago* (L.) L. are only found together in a residual position, or where they have been planted. Competition from allogenic plants (*Agave, Opuntia,* and *Acacia*) is also a serious problem. In the main island of the Madeira archipelago, the laurisilva covered some 60% of the total area but is now reduced to about 16% (10,000 ha) according to Press and Short (1994).

High and Middle Atlas Mountains

Covering an area of around 50,000 km², the High and Middle Atlas ranges are populated by numerous endemics—306 and 237, respectively—according to Enriquez-Barroso and Gomez-Campo (1991). The high rate of endemism is explained by the long isolation of these massifs and their high altitude. But, in addition to this mainly residual flora (Quézel, 1957), there is quite a large number of schizoendemics that demonstrate the role of the Atlas mountains in the neo-speciation process (Gal-

Table 5. Threats affecting the 10 hot-spots in the Mediterranean basin (+: low impact, ++: medium impact, +++: severe impact).

	Fire	Tourism	Overgrazing	Anarchic clear-cutting	Afforestation	Urbanization and industrialization	Land-abandonment, reforestation	Useful plants, crops	Bulbs crops	Competition by introduced plants
Canaries and Madeiran archipelagos		++	+	+	++	++				++
High and Middle Atlas			+++	+++	+++			++		
Baetic-Rifan complex	++	++	++		++	++		++		
Tyrrhenian islands	++	++	+			+	+	++	+	+
Maritime and Ligurian Alps	++	++				+++	++			+
Southern and Central Greece	++	++	++		+	+	+	++		
Crete	++	++	++		++	+		++	+	
Anatolia and Cyprus		+	++	+	++			++	++	
Syria, Lebanon, Israel			+	++	++					
Mediterranean Cyrenaic	+		+++	++	++					

land, 1988). This general region is greatly endangered by anthropization, particularly by overgrazing, land clearance, and anarchical deforestation that lead to desertification, even in the pastures of spiny xerophytes in clumps at high altitude. The balance was disturbed in the 1950s and, for example, land clearance of the Azilal Province alone now reaches 3000 to 5000 hectares per year, with annual erosion of between 5 and 10 m^3 per hectare (Estrade, 1988).

THE BAETIC-RIFAN COMPLEX

Andalusia and the Rif, linked together until the end of the Tertiary era, are grouped together in the same hot-spot because they have great floristic, ecological, and bioclimatic affinities. Around 75% of their total of 3500 species are common to the two regions (Valdès, 1991).

Rif and Tell Coastal Ranges of western Algeria. These two sectors of North Africa have a rich variety of endemics. In the Moroccan Rif range, there are at least 190 endemics, including 50 that are strictly limited to this zone (Enriquez-Barroso & Gomez-Campo, 1991). Unfortunately, this region is subjected to the relentless loss of natural vegetation, particularly due to the illegal growing of hashish. Between 1966 and 1986, the wooded areas and scrublands of the central-western Rif respectively decreased by an average of 42% (989 ha/year) and 38% (2852 ha/year), while cultivated land increased by 93% or 3847 ha/year (Boukil et al., 1987).

In Algeria, the Oranian and coastal sections of the Tell Atlas have, respectively, 91 and 89 endemics (Enriquez-Baroso & Gomez-Campo, 1991). The high rate of endemism reflects the Iberian and Moroccan influences (Quézel, 1964a). There is also strong human pressure, and habitats disappear at a rate that is difficult to estimate (Mathez et al., 1985).

Andalusia. This region of southeast Spain, 87,267 km^2 in area, is unquestionably one of the most important hot-spots of the Mediterranean basin. The complexity of the geologic and climatic history, but also the great diversity of habitats and substrata (including serpentines, dolomites, and gypsum), explain this high biodiversity (Valdès, 1993). Hernández-Bermejo et al. (1993) listed 484 strictly endemic taxa and 465 subendemics in Andalusia, and Gomez-Campo et al. (1984) obtained percentage of endemism greater than 50% in the Serrania de Ronda and in Sierra Nevada. The latter massif contains 177 endemics, including 66 that

are exclusive (Gomez-Campo et al., 1984). Due to this exceptional biodiversity and the serious threats (600 rare taxa, including 68 in danger of extinction, according to Hernández-Bermejo et al., 1993), the local authorities have just recently put in place an integrated conservation plan (Hernández-Bermejo & Clemente-Muñoz, 1993) that aims to limit human activities in the mountain and coastal areas.

MARITIME AND LIGURIAN ALPS

The southwestern end of the alpine range is a noteworthy pole of biodiversity, since around 3100 species and subspecies, including almost 140 endemics, are found in this 9500 km² area (Médail & Verlaque, 1997). This high degree of richness is due to (a) the survival of ancient taxa (much of the region was not affected by the Würm periods of glaciation) facilitated by the diversity of habitats and ecological niches (with a strong altitudinal gradient in a small distance) and (b) the establishment of more recent taxa facilitated by the continuity of the alpine range. With the increase in population and the explosion of tourism along the entire coastline, the most serious dangers again threaten the species of the coast and low altitudes; one example is the disappearance of *Silene sericea* All., an endemic Tyrrhenian psammophilous species.

TYRRHENIAN ISLANDS

The Balearic Islands (except for the Pithyuses, which are biogeographically linked to the Iberian peninsula), Corsica, Sardinia, and Sicily are the remnants of areas that once belonged to the Protoligurian massif (Alvarez, 1976), a Hercynian formation that was fragmented in the Oligo-Miocene, causing migration of the Corso-Sardinian microplate. Only a part of Sicily (Peloritan massif) adjoined the Protoligurian massif in the south, but this island was included in this hot-spot for practical reasons. As a result, these islands have several floristic affinities, even if this Tertiary isolation contributed to the differentiation of neo-endemics that are specific to each area.

Balearic Islands. This archipelago has a relatively limited specific richness, with 180 endemic taxa of which 48 are endangered (Mus, 1995), but only 1 is known to have become extinct: *Lysimachia minoricensis* Rodr., which has, however, been conserved *ex situ*. Tourism and the changes of land use have seriously altered and modified the habitats, particularly coastal communities, low-altitude scrublands, and pine forests. According to a recent study (Mus & Mayol, 1993), 5% of the overall flora of the Balearics is seriously endangered.

Corsica. The flora and vegetation of this island are now well known, particularly after the works of Gamisans (1976–1978, 1991), Gamisans and Jeanmonod (1993), and Contandriopoulos (1962, 1990). In an area of 8748 km², 2354 indigenous taxa are found, with 270 endemics and subendemics, i.e., an 11.5% rate of endemism. The mountain flora includes 39% endemics. Although Corsica's flora seems to be relatively little endangered in the medium and upper altitudes, the situation is clearly more worrying in the coastal fringe, where three quarters of the endemics are endangered. It should be pointed out that 6 of them will probably become extinct, including 2 endemics specific to Corsica, as well as the extremely rare *Naufraga balearica* Constance & Cannon.

Sardinia. Although it is floristically rather poor (ca. 2050 taxa for 24,100 km²), Sardinia deserves to be included in this study because its well-documented endemism (Arrigoni, 1976–1991) is significant (106 endemics s. str.) and there are considerable threats. The low-altitude areas are again the most endangered, but conservation measures are still quite parsimonious, and there are only few reserves (Bocchieri, 1995).

Sicily. Due to its geographical position and contrasting paleogeographical origin, Sicily is an area of major botanical interest, with around 2700 taxa and 310 endemics and subendemics (Verlaque, pers. comm., according to Raimondo et al., 1994, modified). The flora of the hills of Madonia alone includes 50% of Sicily's species and 40 endemics (Brullo et al., 1995) in less than 2% of the island's area. The Etna district contains 21 endemics (Brullo et al., 1995). There are also endemic trees, which is uncommon in the Mediterranean basin: *Abies nebrodensis* (Lojac.) Mattei, which is seriously endangered, *Betula aetnensis* Raf., *Celtis aetnensis* Torn., *Pinus nigra* Arnold subsp. *laricio* Maire, and the recently discovered *Zelkova sicula* Di Pasquale, Garfi & Quézel. The human impact is mainly responsible for the probable extinction of 29 taxa, including 4 Sicilian endemics: *Allium permixtum* Guss., *Anthemis abrotanifolia* (Willd.) Guss., *Carduus rugulosus* Guss., and *Limonium catanense* (Tinbeo) Brullo (Brullo et al., 1995).

SOUTHERN AND CENTRAL GREECE

The Peloponnese, with an area of ca. 21,000 km², contains a total of 2400 species, including 300 Greek endemics, i.e., 12.5% endemism (Iatrou, 1986). Strid (1993) reported 26.5% orophile endemism in the Peloponnese, i.e., 143 endemics;

this reaches 38% if we include the Balkan endemics. The hills that contain the greatest biodiversity are the Taygetos, Chelmos, Parnon, and Killini mountains. The flora of the Peloponnese was affected mainly by north-south migrations and has strong links (130 endemics in common) with the central Sterea Ellas region, which were joined together only 900,000 years ago. In this hot-spot we have included the southern part of this region, from the Karpenision belt, where, in an area virtually the same as that of the Peloponnese, the rate of endemism and the floristic richness are comparable, particularly in the mountain massifs: Parnassos, Giona, Vardoussia, Panaetolicos, Dirphis; rupicolous endemism is more than 10% in almost all of this area, and reaches 20% locally (Quézel, 1964b).

When Greece joined the European Union, its economy swung from an agro-pastoral system to a productivist market economy, which will cause profound changes in the structure and architecture of the ecosystems, and therefore in biodiversity (Margaris, 1992).

CRETE

Crete is well documented from floristic (Turland et al., 1993) and phytoecological viewpoints (Barbero & Quézel, 1980; Zaffran, 1990). Spared by Quaternary glaciations and isolated for around 5 million years, this island has a unique flora, with 171 endemics out of a total of 1706 species and subspecies (Turland et al., 1993) in an area of 8700 km^2. The orophile flora of the three main massifs (Levka Ori, Psiloritis, and Dhikti) is very poor, but of the 217 taxa listed, 44% are endemic (Strid, 1993). In his analysis of the vegetation of Crete's mountains, Zaffran (1982) obtained comparable results: 25 to 40% of endemics for the rupicolous vegetation and 20 to 30% for stripped pastures.

The early colonization by man, about 8000 years ago, profoundly altered the natural balance, with exportation of timber and olives to Egypt between 2500 and 1500 B.C. (McNeely, 1994). Crete still bears the marks of thousands of years of intensive exploitation; forest patches are rare, while the scrublands have a lesser richness and floristic diversity.

ANATOLIA AND CYPRUS

Cyprus. The island of Cyprus, with an area of 9250 km^2, includes 1620 taxa with 170 endemics and subendemics (Alziar, 1995). The most interesting sector is the Troodos massif, where serpentinicole endemism is highly developed, with unique formations of *Cedrus brevifolia* (Hooker fil.) Dode and *Quercus alnifolia* Poech (Barbero & Quézel, 1979) and at least 45 local endemics. The entire island is subjected to major erosion (Tsiourtis, 1993), and mass tourism is developing rapidly on the south coast.

Anatolia. Southern Anatolia, especially the Taurus and Amanus areas, is one of the major centers of biodiversity and endemism in the circum-Mediterranean area. Biogeographical spectra in studies of the vegetation (Quézel, 1973) show that orophile endemism in the Taurus area reaches 20–40% in rupicolous associations, 10–20% in stripped pastures, and 35–70% in culminating screes, with a total of 250 endemics among the 650 species presented in the surveys. Davis et al. (1994) mentioned 2500 species including 250 Turkish endemics in the eastern part of the Taurus area and 3365 species in southwest Anatolia, including 675 Turkish endemics.

Even if the situation of the natural environments is better than in some other areas of the Mediterranean, the human impact is nevertheless perceptible in the overall Amanus/Taurus area. The numerous steppes are the result of continuous human activity, access routes, crop fires, and pasture fires. Land clearance over several centuries has mainly affected the forests of *Pinus nigra* Arnold subsp. *pallasiana* (Lamb.) Holmboe, *Cedrus libani* A. Richard, and *Quercus cerris* L. (Akman et al., 1991), but also the scrublands of endemic *Astragalus* (Demiriz & Baytop, 1985). However, one of the major problems is the intensive harvesting of mainly endemic bulb plants (Oldfield, 1990) for decorative and culinary purposes. Thus, according to Sezik (1989), 57 million tubers belonging to 38 species of orchids are picked annually and are used to prepare "salep," a milk drink.

SYRIA–LEBANON–ISRAEL

The summits of the Lebanon and the Anti-Lebanon ranges (Slenfe-Qammoua, Quriet es Sauda, Ehden Sannin, and Mount Hermon) and their peripheries are areas rich in endemics. One hundred species specific to mount Hermon and the Anti-Lebanon range have been counted (Zohary, 1973), while Auerbach and Shmida (1985) mentioned 47 endemic taxa on the coast of Israel, i.e., a rate of 27%. Nevertheless, the conflict in this region has seriously degraded the phytocenoses of the region, e.g., the formations of *Cedrus libani*. However, precise and recent data on the evolution of the natural environments are not available.

MEDITERRANEAN CYRENAIC

Even if the northern part of the Cyrenaic region does not have a rich flora (1300 species), it still contains no less than 81% of Libya's flora, in only 1.3% of the country's area. The rate of endemism is around 10%, with 137 endemic taxa including 84% of essentially Mediterranean origin (Bartolo et al., 1977, modified). The Djebel Akdhar plays a key role in the area's biodiversity, but the surface area of the natural environments of the "Green Mountain" has been reduced by half (or about 250,000 hectares) in half a century (El'Hamrouni, 1990). Tree-cutting, repeated fires, overgrazing, and mechanical land clearances in low altitudes to extend the orchards and vineyards have strongly altered this Mediterranean enclave.

CONCLUSION

Like the four other mediterranean areas of the world (Cody, 1986), the circum-Mediterranean region is one of the world's major centers for plant differentiation. The assessments mentioned above show that, particularly for the Old World, this region ranks among the most important areas of plant biodiversity. The circum-Mediterranean region alone contains as many species as Europe and Northern Africa combined. Similarly, its high level of endemism is remarkable, and is often equal to that of the world's tropical regions.

In the Mediterranean basin, this richness is not uniformly distributed and the areas of maximum biodiversity, particularly the 10 hot-spots defined here, mainly trace their origins to historical and paleogeographical factors (Pons & Quézel, 1985). The Mediterranean region is an area of refuge but also floral exchange and active speciation (Quézel, 1978, 1985, 1995). In the occidental part of the Mediterranean basin, the maximal biodiversity areas coincide notably (Verlaque et al., in press) with the "Protoligurian massif" and the "Orogenic Belt," which stretched from the Alps to the Baetic mountains during the Oligocene (Alvarez, 1976). The phenomena of stress (Stebbins, 1952), competition, and also the diversity of habitats, with a varied pedological component, explain the region's great richness and its endemism, which is particularly important in the high mountains and in the islands.

However, this biodiversity is now seriously endangered by radically different phenomena that affect the north and south of the basin. The southern countries are subjected to reckless human activity, with overexploitation by man and livestock in all available areas, following an exponential growth in population. On the northern perimeter, however, the virtual abandonment of the agro-sylvo-pastoral system is causing uniformization of the ecosystems and flora, linked to a general biological upsurge, while the coastal areas are ravaged by the spread of mass tourism. In order to counteract this erosion of the phanerogamic biodiversity, it would be necessary to refine the assessments presented in this work and to develop integrated conservation strategies for the identified hot-spots (Falk, 1990), both on the regional level (as has been started in Andalusia, the Balearics, and Corsica) and on national and international levels. We must also emphasize that threatened habitats in need of conservation (e.g., wetlands and coastal habitats) are not necessarily hot-spots of biodiversity. Thus, it is useful to make the distinction between a general need for conservation of endangered habitats, and a more specific need for conserving centers of plant richness and endemism through hot-spots.

In addition, it would be instructive to survey the hot-spots of other taxonomic groups besides plants in order to determine whether the various defined zones coincide. In Great Britain, Prendergast et al. (1993) did not find very close relationships between the hot-spots of the different groups, and this should be tested in the Mediterranean area.

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SURVEY OF CHROMOSOME NUMBERS IN *RUBUS* (ROSACEAE: ROSOIDEAE)[1]

Maxine M. Thompson[2]

ABSTRACT

A literature survey was made of chromosome number counts for *Rubus* species. Numbers are presented for 387 species, representing about 40 percent of the total number, and including 11 of the 12 subgenera. The basic number is universally 7 and ploidy levels include 2*x*, 3*x*, 4*x*, 5*x*, 6*x*, 8*x*, 9*x*, 10*x*, 11*x*, 12*x*, 14*x*, and, questionably, 13*x* and 18*x*. In a few species, more than one chromosome number has been reported. Attempts were made to provide the currently accepted taxonomic designation for each species as well as the outdated synonyms used in original publications. The objective was to provide a summary of available information on chromosome numbers of *Rubus* species and to point out the gaps that need to be addressed.

Rubus is a large and important genus that includes an estimated 900 to 1000 species widely distributed throughout the world. Representatives are found on all arable continents as well as on oceanic islands, and many species provide an important food resource for both humans and animals. Early cytological studies demonstrated that polyploidy has played a significant role in the evolution of this genus (Gustafsson, 1943). The basic number is universally 7 and, currently, ploidy levels are known to range from 2*x* to 14*x*, and possibly 18*x*. The most recent survey of *Rubus* chromosome numbers was included in *Chromosome Numbers of Flowering Plants* (Fedorov, 1969). Since that time, counts for many more *Rubus* species have been published in widely scattered reports. Knowledge of the chromosome numbers of species is important to botanists studying cytotaxonomy, evolution, and phylogenetic relationships and to plant breeders utilizing interspecific hybridization as a breeding procedure.

The exact number of species is unknown because the only comprehensive world taxonomic treatment was published more than 80 years ago (Focke, 1910–1914). During the past eight decades, many new species have been described and, as new evidence has accumulated, many nomenclatural changes made. Recent regional taxonomic studies such as those by Davis (1990), Davis et al. (1967–1970), Edees and Newton (1988), Hogdon and Steele (1968), Kalkman (1984, 1987), Weber (1972, 1981), Weber and Maurer (1991), Yü (1985), and Zandee and Kalkman (1981) have helped clarify the identity of many species in the authors' respective regions. Excluding the subgenus *Rubus*, there are approximately 335 species. For subgenus *Rubus* in Europe, Edees and Newton (1988) gave 300 species in Britain alone (not including the numerous continental species), whereas for this subgenus in eastern North America, Davis (1990) claimed 198 species. Thus, current estimates of the total number of species in the genus *Rubus* may reach 900 to 1000. A comprehensive taxonomic study of this genus is needed to determine more accurately the number of species.

Chromosome number counts for 387 species, representing about 40 percent of the species in the genus, are presented in Table 1, at the end of this article. An additional 75 taxa in subgenus *Rubus* whose names are invalid or whose identities are uncertain are also given because, although not accurately named, they are representatives of the European blackberry flora. Although voucher specimens are reportedly available for some of the species counted, I have made no effort to verify their identity, except for those counted by myself. However, by consulting recent literature and through personal communication with taxonomists specializing in *Rubus*, I have attempted to provide currently accepted names for the species reported. The originally published name is also included so that, in the event that my re-naming is incorrect, a *Rubus* taxonomist could readily identify the species. The number of counts for a species varies from

[1] The author gratefully acknowledges the assistance of the following *Rubus* specialists who kindly reviewed specific subgenera and made valuable nomenclatural suggestions in the early stages of preparation of this manuscript: Heinrich E. Weber for the European blackberries; Mark Widrlechner for North American blackberries; and Naohiro Naruhashi for the subgenus *Ideaobatus*.

[2] 2715 NW Frazier Creek Rd., Corvallis, Oregon 97330, U.S.A.

one to several. In cases where different chromosome numbers are reported for a species, these may be explained by one of the following: one of the counts may represent a variant individual resulting from spontaneous doubling of chromosomes at some early stage of development or from the union of an unreduced gamete with a reduced gamete, a common phenomenon in this genus; they may actually represent populations within a species that have different ploidy levels; or they may be the result of mistaken identification by an author.

In the discussion and in Table 1, the species, chromosome numbers, and reference citations are arranged according to the subgenera established by Focke (1910–1914), except for *Micranthobatus*, whose species have been separated out of *Lampobatus* by Kalkman (1987), and *Dalibarda*. Since most of the species placed in subgenus *Dalibarda* by Focke (1910–1914) have been transferred to subgenus *Cylactis* and *R. dalibarda*, itself, has been moved to a different genus, as *Dalibarda repens* L. (Bailey, 1941), the continued acceptance of *Dalibarda* as a subgenus is questionable. In Table l, the currently accepted name is given first, synonyms are indented under the valid name, and names indented, in parentheses, and preceded by "as" indicate that in the original publication, identification was incorrect but, subsequently, the plant was reidentified. Eleven of the 12 subgenera are represented: only *Lampobatus* sensu stricto remains to be studied.

Subgenus *Chamaemorus*

The chromosome number of *R. chamaemorus*, the only species in this subgenus, is well established with 18 hexaploid counts.

Subgenus *Chamaebatus*

Of about six species in this subgenus, three have been counted: *R. calycinus* and *R. pectinellus* are hexaploid, whereas *R. nivalis* is diploid.

Subgenus *Comaropsis*

Only one of the two species in this subgenus has been counted: *R. geoides* is tetraploid.

Subgenus *Cylactis*

There are chromosome number counts for 10 of the appproximately 16 species now included in this subgenus. Six of these, *R. lasiococcus, R. pedatus, R. pubescens, R. pseudojaponicus, R. stellatus,* and *R. subarcticus* are diploid. *Rubus arcticus* which, with several counts, is no doubt predominately diploid, was found to have a distinct triploid population (Johnson & Packer, 1968). Zhukova (1980) also reported triploidy for this species. It is not uncommon that diploid species give rise to an occasional triploid or tetraploid individual which may, through vegetative reproduction or apomictic seeds, spread to form colonies or populations of considerable extent. In the case of *R. humulifolius*, more information is necessary to determine whether this species is mainly diploid (two counts) or tetraploid (one count). However, for *R. nepalensis*, the three tetraploid counts, as compared to only one diploid, suggest that it may be principally a tetraploid species. With 14 counts, *R. saxatilis* is well established as a tetraploid species.

Subgenus *Orobatus*

Of the approximately 18 species in this exclusively South American subgenus, 6 have been counted and all are hexaploid. These include the relatively weak-growing plants of *R. acanthophyllus, R. coriaceus,* and *R. glabratus,* as well as the very vigorous species *R. macrocarpus, R. nubigenus,* and *R. roseus,* which is also vigorous and has robust canes to 6 m or longer. This high chromosome number contrasts with the consistent diploid number in the blackberries (subg. *Rubus*) that occur in the same Andean region as the *Orobatus* species.

Subgenus *Dalibardastrum*

Three of the 10 to 12 species in this subgenus have been counted and all are polyploid; *R. tricolor* and *R. tsangorum* are tetraploid, whereas *R. amphidasys* is hexaploid.

Subgenus *Malachobatus*

When Fedorov (1969) published his *Rubus* chromosome number survey, only seven species in the *Malachobatus* had been counted. Currently, 40 (31%) of the estimated 127 species have been counted. Thus far, all species in this subgenus are polyploid: there are twenty-seven 4*x*, five 6*x*, six 8*x*, and two 14*x* species. Although there are seven diploid counts, this ploidy level is not consistent with other information. Four of the species reportedly diploid were found to be high polyploids by other investigators: *R. fairholmianus* was octoploid (Nybom, 1986); *R. gardnerianus* was octoploid (Gill et al., 1984; Singhal et al., 1990); *R. rugosus* was both octoploid (Iwatsubo & Naruhashi, 1992) and 14*x* (Nybom, 1980, 1986; Thompson, 1995a); and *R. hayata-koidzumi* was tetraploid (Iwatsubo & Na-

ruhashi, 1993; Thompson & Zhao, 1993). Of the other three doubtful diploid species, two have sole counts, namely, *R. fulvus* and *R. micropetalus* by Subramanian (1987), and the third, *R. paniculatus*, has two counts (Malik, 1965; Mehra & Dhawan, 1966). The identity of all species with diploid counts needs to be verified and their counts reconfirmed before it can be concluded that diploid species occur in this predominately polyploid subgenus.

Omitting the discrepant diploid counts, there appear to be three species in which two different numbers actually do occur. Naruhashi and Iwatsubo (1993) reported that two forms, both hexaploid and octoploid, are commonly found in both *R. hakonensis* and *R. buergeri*. For *R. rugosus*, there is one octoploid and three 14*x* counts. These two different counts for *R. rugosus*, along with the ploidy levels reported for its close relative, *R. moluccanus* (4*x*), and *its* allies *R. multibracteatus* (4*x*), *R. hillii* (6*x*), *R. fairholmianus* (8*x*), possibly *R. indicus* (8*x*), and *R. glomeratus* (14*x*), suggest that this group of species represents a polyploid complex. Further cytotaxonomic studies are necessary to clarify the relationships among these species.

Thus far, there is no evidence for apomixis among the *Malachobatus* polyploid species. Nybom's (1986) demonstration of sexual reproduction in two species, *R. fairholmianus* and *R. rugosus*, needs to be expanded to other species in order to determine if this is the predominate mode of reproduction in this subgenus. The existence of relatively clear-cut species boundaries supports the concept that hybridization and apomixis have not played an important evolutionary role, if any, as they have in *Rubus*, the other major polyploid subgenus.

Subgenus *Anaplobatus*

In this small subgenus of possibly five to six species, the four species counted are all diploid. *Anoplobatus* is closely related to the predominately diploid *Idaeobatus*. The sole triploid report for *R. deliciosus* by Longley (1924) was no doubt an aberrant individual or possibly an interspecific hybrid.

Subgenus *Idaeobatus*

Counts have been reported for 70 (52%) of the estimated 135 species in this subgenus. Fifty-five of these are reported only as diploids; nine of them are reported as both diploid and other ploidy levels; four are reported as tetraploid only; one as ca. 13*x*; and one as 18*x*. The nine species that are reported as diploid plus other counts are probably basically diploid, with the other counts, triploid or tetraploid, merely cytological aberrant individuals or colonies. The single triploid count for *R. strigosus*, which is a well-established diploid species, as well as the sole triploid counts for the diploid species *R. parvifolius* and *R. yoshinoi*, represent aberrant individuals which arose from union of a reduced and an unreduced gamete (Naruhashi & Iwatsubo, 1993). Spontaneous chromosome doubling in zygotes or in somatic tissues to form tetraploid individuals is also not uncommon. The tetraploid counts for the basically diploid species *R. foliolosus*, *R. hypargyrus*, and *R. niveus* are most likely aberrant individuals of this type. The chromosome numbers above diploid reported for the South African species *R. apetalus* (2*x* and 4*x*), *R. longipedicellatus* (2*x*, 4*x*, and 5*x*), and *R. pinnatus* (2*x* and 4*x*) have been explained by Spies and DuPlessis (1985) as having arisen through interspecific hybridization and introgression, accompanied by doubling of chromosomes. The primary basic number for these species is considered to be diploid. Altogether, it appears that 63 (90%) of the 70 *Idaeobatus* species counted are basic diploid species.

The four species for which only tetraploidy has been reported include *R. leucocarpus*, *R. nishimuranus*, *R. probus*, and *R. sachalinensis*. These species arose recently enough that their progenitors have, with a certain degree of certainty, been ascertained or can be postulated. With no knowledge of the chromosome number, Focke (1910–1914) considered *R. leucocarpus* to be a subspecies of *R. niveus* Thunb. and mentioned that it differs from the typical species in its larger flowers and fruits and its more robust plant, traits that are characteristic of autotetraploids. Thus, it is probable that this species arose directly from *R. niveus*. The suspected hybrid origin of the tetraploid *R. nishimuranus* has been confirmed by Naruhashi (1976) and Naruhashi and Iwatsubo (1993), who concluded that this species is an allopolyploid derived from a cross of *R. trifidus* × *R. hirsutus*. The third tetraploid *Idaeobatus* species, *R. probus*, was recently reported (as *R. muelleri*) by Thompson (1995a), who made counts on three plants from Australia; two plants from one source and one plant from another. Because this species is so similar to *R. fraxinifolius*, Australian botanists have disagreed as to whether it should be included in that species or considered a separate species. The tetraploid count of *R. probus* provides another trait, in addition to minor morphological traits, that may help to distinguish these two species; that is, if *R. fraxinifolius* is diploid, as suspected. It is not possible to claim, although in-

teresting to speculate, that *R. probus* may be an autopolyploid derivative of *R. fraxinifolius*. The fourth tetraploid *Idaeobatus* species, *R. sachalinensis*, which is widely distributed in northeast Asia, was demonstrated by Rozanova (1939) to have arisen through autopolyploidy from *R. idaeus*. In northeast Asia, *R. idaeus* varieties *melanolasius* and *sachalinensis* (both now included in *R. sachalinensis*) are tetraploid. However, the forms to which these varietal names have been applied in northwestern North America (included here as synonyms of *R. strigosus*) are diploid. Although not given in Table 1, several polyploid raspberry cultivars (*R. idaeus*) have arisen spontaneously, e.g., the triploid 'November Abundance', 'Belle de Fontenay', and 'All Summer' (Darrow, 1937) and the tetraploid 'Colossus', 'Hailshamberry', and 'LaFrance' (Jennings, 1988).

The most puzzling reports for this almost universally diploid subgenus are the very high ploidy counts reported for two *Rubus* sp. in the mountains of New Guinea by Borgmann (1964). Fortunately, Borgmann (1964) cited voucher specimens for these unknown *Rubus* species and C. Kalkman, of the Rijksherbarium in Leiden, the Netherlands, very kindly provided me with the identification of these as well as Borgmann's (1964) other unknown species with chromosome counts (C. Kalkman, pers. comm.). The *Idaeobatus* species are *R. archiboldianus* ($2n$ = ca. 91) and *R. lorentzianus* ($2n$ = 126). Both of these counts are highly suspect. Zandee and Kalkman (1981) mentioned only nine *Idaeobatus* species in New Guinea. Based on their relationships, six of these would be expected to be diploid; *R. fraxinifolius* and *R. chrysogaeus* are related to *R. rosifolius* ($2x$); and *R. ferdinandi-muelleri*, *R. papuanus*, and *R. montis-wilhelmi* ($2x$) are closely related enough to be considered a species complex. The chromosome number for the ninth species, *R. macgregorii*, has not been reported. These extraordinarily high chromosome numbers definitely need confirmation, as well as counts made for the other species in New Guinea, before an attempt can be made to hypothesize how two species with such high ploidy levels of $13x$ and $18x$ could have evolved from the surrounding species that are most likely diploids. It is possible that cytological preparations of these *Rubus* sp. may have been mislabeled. If the count really was of a *Rubus* species, this high number may belong to an unknown *Malachobatus* species because polyploidy is common in this subgenus, with levels reaching $14x$ ($2n$ = 98).

Subgenus *Micranthobatus*

Of about 12 species in this subgenus, chromosome numbers have been counted for 5: *R. cissoides*, *R. parvus*, *R. schmidelioides*, and *R. squarrosus* from New Zealand and *R. royenii* var. *hispidus* from New Guinea are all tetraploid.

Subgenus *Rubus* (European blackberries)

The major challenge in this subgenus is not cytological but rather taxonomical. For over 200 years, and continuing today, numerous taxonomists have described and named a few thousand species in this very complex group. The massive array of variation that exists results from the reproductive processes characteristic of this group. Except for the few sexual diploid species, most species are facultative apomicts that can freely hybridize, even with rather distantly related species. In addition to sexual reproduction, segregating offspring may arise through a subsexual process involving normal meiosis in the embryo sac, followed by fusion of two of the resultant haploid cells. However, the predominate mode of reproduction is pseudogamy. Although pollination is necessary to initiate development, the embryo is strictly maternal, which provides a mechanism for wide distribution of a uniform genotype. In this subgenus, there is an equilibrium system in succeeding generations with alternating apomictic and sexual reproduction, which provides for both segregation and rapid, extensive dispersal of a single genotype. Depending upon its adaptability, this "clone" may occur as a local variant in a limited area only or it may become very widespread, thus simulating a true species. Dispersal is accelerated further by the universal propensity for vegetative propagation. These processes have combined to cause a blurring of conventional species boundaries, which accounts for the numerous nomenclatural discrepancies among taxonomists and the thousands of names that have been proposed and subsequently discarded. Although there are some species that are widely distributed and morphologically distinct enough to be recognized by all botanists, there are many more forms where boundaries are not so clear-cut. It is unlikely that an exact number of species will ever be universally accepted.

Plants with aberrant chromosome numbers may arise through parthenogenesis to give haploid plants, by meiotic disturbances that result in aneuploids, from unreduced gametes that give rise to offspring with increased chromosome numbers, or by spontaneous doubling of chromosomes in somatic cells.

Many of the chromosome counts presented in Table 1 were made many years ago when a different classification and nomenclatural system was in vogue. Heslop-Harrison's (1953) major cytological study of this group relied upon the species designations of W. C. R. Watson, the authority for British *Rubus* taxonomy at that time (Watson, 1958). Subsequently, Edees and Newton (1988) reassessed this genus in Britain and have discarded, for various reasons, many species names applied by Watson. Therefore, many of Heslop-Harrison's chromosome counts were made on taxa whose identity is now questionable. Gustafsson (1943) summarized his and others' counts for European blackberries and, although some of his Scandinavian species have been revised, in several cases the current synonymy is known so the counts can be presented for validly named species. In other cases, names were applied to local forms without proper documentation; these have been relegated to uncertain identity or invalid species names. Principal authorities used to establish current nomenclature in the European blackberries were Weber (1972), Weber (1981), H. E. Weber (pers. comm.), and Edees and Newton (1988), although I take full responsibility for all errors in interpretation.

Chromosome numbers are reported here for 194 species of European blackberries with my concept of currently accepted nomenclature (while recognizing that there may not be general agreement among taxonomists about these names). Since the cytological situation differs somewhat in the two major sections of this subgenus in Europe, they will be treated separately.

In section *Rubus*, chromosome counts of 154 species are summarized. Only three (2%) basic diploid species have been documented; *R. canescens*, *R. ulmifolius*, and its close relative, *R. sanctus*.

Six (4%) species are reported to be triploid; *R. divaricatus* (as *R. nitidus* complex), *R. grabowskii* (as *R. thrysoideus* complex) and its close relatives, *R. elatior* and *R. montanus*, are all well established as triploid species (Gustafsson, 1943). The sole count of tetraploid for *R. divaricatus* is either an error or an aberrant individual. *Rubus brevistaminosus* and *R. hylophilus*, with only one triploid count each, need confirmation.

With 125 species counted only as tetraploid, this is clearly the predominate ploidy level in this section. Intraspecific chromosome number variation is reported for 14 species, all of which have at least one tetraploid count. The one diploid count in *R. infestisepalus* was interpreted by Heslop-Harrison (1953) to be a haploid variant in this tetraploid species. The triploid count for *R. fissus*, reported by Beijerinck (1956), was made on a single plant and contrasts with the other tetraploid counts for this species. *Rubus leucostachys*, with one triploid count and one tetraploid, remains to be clarified. Six species are given as both tetraploid and pentaploid; *R. drejeri*, *R. formidabilis*, *R. hartmanii*, *R. lentiginosus*, *R. milesii*, and *R. pedemontanus*. Except for *R. pedemontanus*, the chromosome numbers of these species need to be reappraised. Although Gustafsson (1943) considered *R. pedemontantus* (as *R. bellardii*) to be a uniform, widespread, and well-established pentaploid species and dismissed the tetraploid count in Maude (1939) as an error, two additional tetraploid counts have been subsequently reported. Czapik (1987) specifically mentions two chromosome races for *R. bellardii* in Europe. Also, it may be that the two different counts given for *R. pedemontanus* can be accounted for by the fact that *R. bellardii* is synonymous only in part with *R. pedemontanus* and that I have erroneously synonymized all *R. bellardii* reports. Four species are reported as both tetraploid and hexaploid: *R. infestus*, *R. newbridgensis*, *R. nitidiformis*, and *R. pyramidalis* var. *parvifolius*. Heslop-Harrison (1953) explained that the hexaploid count for *R. pyramidalis* var. *parvifolius* was clearly an aberrant seedling, probably resulting from an unreduced gamete, because determinations from the adult plant were all tetraploid. It is possible that a similar explanation may account for the single hexaploid counts for *R. infestus*, *R. newbridgensis*, and *R. nitidiformis*. In the absence of any well-established hexaploid species in this section, it is most likely that the primary number for all species where these two different counts are given is basically tetraploid and that other counts are due to occasional aberrant plants or to errors in identification. Additional counts are necessary to verify this supposition. Altogether, if species with both tetraploid and other counts (except for the triploid *R. divaricatus*) are added to those with only tetraploid counts, 139 of the 154 (90%) of the species in this section are tetraploid.

Five (3%) of the species are reported to be pentaploid: *R. anglocandicans*, *R. marshallii*, *R. kollundicola*, *R. pedemontanus*, and *R. vestervicensis*. There are only single counts for the first two species and, in fact, Heslop-Harrison (1953) suspected that the single plant of *R. marshallii* counted was actually a large form, not typical of the species. Thus, these two species need confirmation. The other three have been well documented by Gustafsson (1943) as pentaploid. Of these pentaploid species, only *R. pedemontanus* is widely distributed in Eu-

rope; the others are local endemic forms in Britain and in Sweden.

The only hexaploid count for a species in the section *Rubus* is a single count for *R. bloxamianus* in Maude (1939) which, without confirmation, may be considered an aberrant individual or an error. Both Gustafsson (1943) and Heslop-Harrison (1953) concluded that, except for a possible aberrant individual, hexaploid species are not found in this section. This conclusion has been substantiated in subsequent studies.

In section *Corylifolii*, as in section *Rubus*, tetraploidy is the predominate chromosome number. However, this section differs cytologically in several respects: there are no diploid species, there are relatively more pentaploid species, there are a few hexaploid species, a few species have two cytotypes, and there are a few aneuploids.

The lack of diploids is to be expected since Lidforss (1914) postulated that species in this section were primary and secondary hybrids and segregation products of crosses between the tetraploid *R. caesius*, a species currently placed in its own, monotypic section, *Caesii*, and species in section *Rubus*. The *Corylifolii* species are not as numerous nor as widely distributed as species in section *Rubus* and species boundaries are even less distinct, as evidenced by the relatively large number of varieties described for some species (Gustafsson, 1939).

Of the 38 species counted, 17 (45%) are given as tetraploid only and 8 (21%) as pentaploid only. Four (10%) are well documented as hexaploid only. The fact that the hexaploid species are few in number and have rather limited distribution suggests that this ploidy level is not well developed. Gustafsson (1939) presented evidence that in nine (24%) of the *Corylifolii* species, populations do occur with different chromosome numbers. His results are creditable not only because of his knowledge of the species identity, but also because he made several counts on samples from different populations. *Rubus camptostachys* was $4x$, $6x$ and aneuploid ($\pm$ 30); *R. dissimulans* varieties were $4x$, $6x$ and aneuploid ($\pm$ 42); *R. eluxatus* was $4x$ and aneuploid ($\pm$ 28 and $6x + 3$); *R. fasiculatus* was $4x$, $5x$, $6x$, and aneuploid ($4x + 1$); *R. gothicus* was $4x$, $5x$, and $\pm$ 28; *R. lidforssii* was $4x$ and $5x$; *R. lindbloomii* was $4x$ and $6x$; *R. nemorosus* was $4x$ and $5x$; and *R. norvegicus* was $4x$, $5x$, and $6x$. The counts of both tetraploid and hexaploid reported for *R. conjungens* by Heslop-Harrison (1953) were not explained as representing different populations, so it is not clear if the hexaploid count reflects a different cytotype or merely an aberrant individual.

Counts for 75 "species" in both sections *Rubus* and *Corylifolii* classified as "doubtful determination and/or taxonomic status" are presented here, but separately because, regardless of their true identity, these data add to the cytological picture of the group as a whole in Europe. These include many counts for British plants to which valid continental species' names had been erroneously applied, local forms that had originally been given species rank but are no longer accepted as such, aggregate species such as *R. hirtus*, as well as forms to which names were applied but never documented.

Subgenus *Rubus* (North American Blackberries)

Chromosome numbers in the North American blackberries were studied most intensively in the East by Longley (1924) and Einset (1947), and in the West by Fischer et al. (1941), Darrow and Longley (1933), Brown (1943), and Zielinski and Galey (1951). In comparing the blackberries of eastern North America with those of Europe, some similarities and differences may be mentioned. One similarity is the important evolutionary role of interspecific hybridization and facultative apomixis so that species boundaries are difficult, if not impossible, to define accurately. Another commonality is the significance of polyploidy in speciation, although the eastern North American group represents an even wider range of ploidy levels, including $2x$, $3x$, $4x$, $5x$, $6x$, $7x$, $8x$, $9x$ and even one aneuploid ($5x + 1$) species. Also similar is the common association of facultative apomixis (pseudogamy) with polyploidy (Einset, 1951). One significant difference is the existence of several, apparently sexual, diploid species compared to only three diploids among the several hundred species of blackberries in Europe. Also, whereas tetraploid is the dominant ploidy level in the European blackberries, this number appears to be relatively less common in the North American species. From the limited counts available for eastern North American species, it appears that, except for the section *Flagellares* where ploidy levels higher than tetraploid are common, the most frequent numbers reported are diploid and triploid.

The most recent attempts to clarify the taxonomy of the eastern North American blackberries were those of Davis et al. (1967–1970), updated by Davis (1990), and Hogdon and Steele (1968). Species listed in Table 1 follow the Davis et al. (1967–1970) treatment (with modifications suggested by Mark Widrlechner, pers. comm.) because it includes all of the eastern North American species,

whereas Hogdon and Steele (1968) dealt only with those of the New England states. It is suspected that the widely varying chromosome numbers reported for some species can be partly attributed to misidentification of the plants. However, that varying chromosome numbers may exist in wild populations is demonstrated by Einset's (1951) comprehensive study of chromosome numbers of offspring following self-pollination, controlled cross-pollinations, and open pollinations of plants with established numbers. An individual polyploid plant ($3x$, $4x$, $5x$, $5x + 1$, $7x$, or $9x$) produced not only apomictic offspring resembling the maternal plant in morphology and chromosome number but also parthenogenetic haploids and true hybrids with varying chromosome numbers as a result of different combinations of reduced and unreduced gametes. The extent to which these deviant chromosome number forms survive and spread in nature depends upon their level of apomixis and/or success of vegetative propagation, their adaptability, and their ability to compete as compared to the species norm from which they were derived.

Chromosome counts have been reported for 45 (22%) of the approximately 200 species of eastern North American blackberries. However, it is clear from Table 1 that the information is scanty, with only a single count for most species, and that there is a very inconsistent pattern in the numbers reported for some species. More cytological information is necessary to determine how much valid intraspecific variation in chromosome number actually does exist. Unfortunately, there have been no significant cytological studies to expand and corroborate the early work of Longley (1924), many of whose plants have suspect identity. The following is an attempt to summarize the limited cytological information for each section.

In section *Alleghenienses,* chromosome counts are $2x$, $3x$, and $4x$. *Rubus allegheniensis* appears to be a well-defined diploid, sexual species. Aalders and Hall's (1966) diploid count for *R. allegheniensis* represented 22 different clones in southwest Nova Scotia. These authors counted chromosomes and studied morphological traits of 470 blackberry plants collected throughout Nova Scotia. They concluded that there were two distinct diploid species, *R. allegheniensis* and *R. hispidus,* and that 355 of the plants studied were triploid hybrids and the remaining 52 were $4x$, $5x$, or $6x$, probably derived from further hybridizations and unreduced gametes. The polyploids all appeared to be facultatively apomictic, which would account for the perpetuation of so many triploid clones. Based on morphological criteria, these triploids were interpreted as having been derived from hybridization of the two basic species, with one of them contributing an unreduced gamete. This study demonstrates the cytotaxonomical complexity facing a botanist attempting to classify the blackberries into discrete species. The two triploid counts for *R. allegheniensis* by Longley (1924) and Einset (1947) most probably were from aberrant plants arising from an unreduced gamete. It is interesting to note that, although *R. allegheniensis* is considered to be a good diploid species, several *allegheniensis*-type tetraploid cultivars (e.g., 'Lawton', 'Ancient Briton', 'Snyder', 'Taylor', and 'Eldorado') have been selected directly from wild populations, although some have been speculated to be interspecific hybrids. In fact, the lineage of the modern eastern upright blackberry cultivars, all tetraploids, traces back to these early wild selections. Obviously, tetraploid forms do appear in nature and, at least some of them, are superior enough in horticultural traits to have been selected for human usage. Because they do not appear to have become a significant part of the population, the question arises about their relative adaptablility in nature as compared to the diploids.

In section *Arguti,* $2x$, $3x$, $4x$, $5x$, $5x + 1$, and $6x$ counts have been reported for various species. I will make no attempt to summarize these because I suspect that the erratic cytological picture reflects misidentified plants in too many cases. It is probable that *R. argutus* is a diploid species, with an occasional triploid aberrant.

The section *Canadenses* is represented here by *R. canadensis.* Craig (1960) reported triploidy in 13 individual clones collected in seven regions of New England, New Brunswick, and Nova Scotia. With three other authors' triploid counts and Einset's (1951) demonstration of apomixis in triploid *R. canadensis,* it appears that this cytotype prevails in a significant part of the range of this species. The three reports of diploid forms indicate that there are also diploid populations.

In section *Cuneifolii,* there are counts of $2x$, $3x$, and $4x$. *Rubus cuneifolius* is a diploid species. Based on meiotic pairing relationships, Spies and DuPlessis (1985) interpreted their individual triploid and tetraploid plants as autopolyploids of the diploid species. These authors made the same conclusion about the triploid and tetraploid *R. pascuus* plants although, in this case, no diploid species was observed.

Section *Flagellares* is the only group in eastern North America in which most species have been consistently reported to be polyploid. I suspect that Longley's (1924) diploid counts for *R. recurvicaulis*

and triploid for *R. biformispinus* and *R. multiformis* were based on misidentified plants. Because many of Longley's (1924) chromosome counts are inconsistent with those of others, the identifications of his plants are highly suspect. The remainder of the counts for this section are 4*x*, 5*x*, 6*x*, 7*x*, 8*x*, and 9*x*, which, if these plants were correctly identified, is strongly suggestive of a polyploid complex similar to that of *R. ursinus* in western North America.

In the section *Hispidi*, 2*x*, 3*x*, 4*x*, 5*x*, and 8*x* counts are reported. Aalders and Hall's (1966) diploid counts for 41 clones of *R. hispidus* collected widely in southwestern Nova Scotia, along with Thompson's (1995a) diploid count from a North Carolina plant, suggest that this is a widespread basic diploid species. It is most likely that Longley's (1924) pentaploid and octoploid counts for *R. hispidus* were mistakenly identified plants, possibly belonging to section *Flagellares*, which has a trailing plant growth habit like the *Hispidi* but, unlike *Hispidi*, is characterized by higher ploidy levels. There is one count each for *R. huttonii* (4*x*), *R. plus* (3*x*), *R. signatus* (3*x*), and *R. tardatus* (3*x*).

In section *Setosi*, chromosome numbers reported are 2*x*, 3*x*, 4*x*, and 5*x*. *Rubus setosus* has both diploid and triploid counts, but with such a limited sampling it is not possible to determine the relative abundance of each of these ploidy levels. There is one count each for *R. dissensus* (3*x*), *R. glandicaulis* (3*x*), *R. clandestinus* (4*x*), *R. hanesii* (4*x*), *R. miscix* (3*x*), *R. notatus* (2*x*), and *R. wisconsinensis* (5*x*).

For section *Triviales*, the only species counted, *R. trivialis*, has been consistently given as diploid by six investigators. There seems to be no question about this being a widespread, basic diploid species.

Although limited cytological information is available for the eastern North American blackberries, a few tentative conclusions are warranted. It appears that, in each section, there is at least one easily recognized species, i.e., the one after which the section is named. Seven of these, *R. alleghaniensis*, *R. argutus*, *R. canadensis*, *R. cuneifolius*, *R. hispidus*, *R. setosus*, and *R. trivialis*, are basically diploid but may have triploid or tetraploid individuals or populations as well. By contrast, the eighth one, *R. flagellaris*, is polyploid, with the predominate chromosome number unknown due to discrepant counts and insufficient sampling. Because of the discrepancies in chromosome numbers, even within species, counts need to be made on population samples rather than individual plants. Such counts made in conjunction with a taxonomic reappraisal would greatly contribute to the clarification of the blackberry species of eastern North America.

The section *Ursini*, represented only by *R. ursinus*, is geographically isolated from all other North American blackberries. It occurs only in the western parts of the Pacific States from southern California to southern British Columbia and in western Idaho. Brown (1943) made an intensive cytotaxonomic study of this species in the southern half of its range and concluded that there were two main chromosome numbers: octoploidy was dominant in most of California, whereas 12*x* was dominant from northern California to southern Oregon, and presumably northward. The limited numbers of plants found with 9*x*, 10*x*, or 11*x*, were assumed to have been derived from the two main chromosome types through hybridization. The relatively few oddploids found suggested that apomixis is not an important mode of reproduction in this species. The lack of consistent morphological traits associated with chromsome number led Brown (1943) to conclude that this western blackberry population consists of only one species with six different ploidy levels.

Subgenus *Rubus* (South American Blackberries)

Of Focke's (1910–1914) four sections of *Rubus* in South and Central America, i.e., *Dissitiflori*, *Xerocarpi*, *Duri*, and *Floribundi*, chromosome counts have been reported for species only in the *Floribundi*. Thus far, the information is very limited, with only one diploid count each for *R. adenotrichos*, *R. robustus*, and *R. urticifolius*, and two for *R. bogotensis*. Should further studies confirm the lack of polyploidy in these blackberries, this cytological situation is a striking contrast to that of this subgenus in North America and Europe.

Proposed Natural Inter-Subgeneric Hybrid

Tetraploid *R. glaucus*, both cultivated and in the wild, is widespread in the northern Andean countries and in Central America. Darrow (1952) first suggested that this species was an allopolyploid originating from hybridization between a black raspberry and a South American blackberry. Jennings's (1978) studies on anthocyanin pigments in *R. glaucus* and its putative parents provided support for this concept.

In conclusion, this compilation provides scientists working with this genus convenient access to the chromosome numbers of species published to date. The current state of knowledge is presented,

and the gaps that need further investigation are made evident. Although counts have been made on an estimated 40 percent of *Rubus* species, many of these are single counts that need confirmation, and the chromosome numbers of the remaining 60 percent of the species need to be determined. It is hoped that this paper will stimulate an interest in additional cytological and taxonomical studies that will contribute to the elucidation of the nature of the species in this large and complex genus.

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Table 1. Chromosome numbers of *Rubus* species. See page 129 for further explanation.

Taxon	2*n*	References
	Subgenus *Chamaemorus* (Hill) Focke	
R. chamaemorus L.	56	Longley 1924; Darrow & Longley 1933; LaCour (Maude 1939); Löve & Löve 1944; Heslop-Harrison 1953; Vaarama 1954; Larsson 1957, 1969; Jørgensen et al. 1958; Sokolovskaya & Strelkova 1960; Löve & Ritchie 1966; Laane 1969; Skalinska et al. 1978; Engelskjon 1979; Löve & Löve 1982a; Zhukova 1982; Krogulevich & Rostovtseva 1984; Dmitrieva & Parfenov 1985
	Subgenus *Chamaebatus* Focke	
R. calycinus Wall. ex D. Don	42	Sharma & Sarkar 1970
R. nivalis Douglas ex Hook.	14	Thompson 1995a
R. pectinellus Maxim.	42	Jinno 1951a, 1958; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
	Subgenus *Comaropsis* Focke	
R. geoides Sm.	28	Haskell & Paterson 1966
	Subgenus *Cylactis* Focke	
R. arcticus L.	14	Vaarama 1939; Larsson 1957, 1969; Sokolovskaya & Strelkova 1960; Johnson & Packer 1968; Kotimäki & Hiirsalmi 1979; Belyaeva & Siplivinskiy 1975, 1981; Yurtsev & Zhukova 1982; Thompson 1995a
R. arcticus L.	21	Johnson & Packer 1968; Zhukova 1980
R. arcticus L. subsp. *acaulis* (Michx.) Focke	14	Löve & Löve 1982a
acaulis Michx.	14	Löve & Ritchie 1966
acaulis Michx.	21	Zhukova 1982
Cylactis arcticus (L.) Raf. subsp. *acaulis* (Michx.) W.A. Weber	14	Löve 1987
R. arcticus L. subsp. × *stellarcticus* G. Larsson	14	Thompson 1995a
R. humulifolius C.A. Mey	14	Rostovtseva 1977; Krogulevich & Rostovtseva 1984
R. humulifolius C.A. Mey	28	Vaarama 1939
R. lasiococcus A. Gray	14	Thompson 1995a
R. nepalensis (Hook. f.) Kuntze	28	Gustafsson 1939; Thompson 1995a
R. nutans Wall.	14	Malik 1965
R. nutans Wall.	28	Mehra & Dhawan 1971
R. pedatus Sm.	14	Taylor & Mulligan 1968; Sokolovskaya et al. 1985; Iwatsubo & Naruhashi 1992; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. pubescens Raf.	14	Löve 1954; Vaarama 1954; Löve & Löve 1966, 1982a, b; Thompson 1995a
Cylactis pubescens (Raf.) W.A. Weber	14	Löve 1987
R. psuedojaponicus Koidz.	14	Iwatsubo & Naruhashi 1993
R. saxatilis L.	28	Scheerer 1939; Vaarama 1939, 1954; Löve & Löve 1944; Löve 1954; Larsson 1957, 1969; Sorsa 1963; Krogulevich 1978; Skalinska et al. 1978; Engelskjon 1979; Löve & Löve 1982b; Dmitrieva & Parfenov 1985
Cylactis saxatilis (L.) Löve	28	Löve 1987
R. stellatus Sm.	14	Vaarama 1954; Larsson 1957, 1969; Kotimäki & Hiirsalmi 1979
R. subarcticus (Greene) Rydb.	14	Longley 1924
Subgenus *Orobatus* Focke		
R. acanthophyllus Focke	42	Thompson 1995a
R. coriaceus Poir.	42	Thompson 1995a
R. glabratus Kunth	42	Thompson 1995a
R. macrocarpus Benth.	42	Dale & Ingram 1981
R. nubigenus Kunth	42	Thompson 1995a
R. roseus Poir.	42	Thompson 1995a
Subgenus *Dalibardastrum* (Focke) Yü & Lu		
R. amphidasys Focke ex Diels	42	Thompson & Zhao 1993
R. tricolor Focke	28	Keep 1958; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. tsangorum Hand.-Mazz.	28	Thompson 1995a
Subgenus *Malachobatus* Focke		
R. acuminatus Sm.	28	Malla et al. 1975; Iwatsubo & Naruhashi 1992
R. assamensis Focke	28	Thompson & Zhao 1993
R. bambusarum Focke	28	Thompson & Zhao 1993
R. henryi Hemsl. & Kuntze var. *bambusarum* (Focke) Rehder	28	Keep 1958
R. buergeri Miq.	42	Naruhashi & Iwatsubo 1993
R. buergeri Miq.	56	Jinno 1951a, 1958; Britton & Hull 1957; Iwatsubo et al. 1992; Naruhashi & Iwatsubo 1993; Thompson & Zhao 1993
R. caudifolius Wuzhi	28	Thompson & Zhao 1993
R. chroosepalus Focke	28	Thompson & Zhao 1993

Table 1. Continued.

Taxon	2*n*	References
R. crassifolius Yü & Lu	28	Thompson & Zhao 1993
R. dolichophyllus Hand.-Mazz.	28	Thompson & Zhao 1993
R. echinoides Metc.	28	Thompson & Zhao 1993
R. fairholmianus Gardner	14	Subramanian 1987
R. fairholmianus Gardner	56	Nybom 1986
R. feddei Lév. & Vaniot	28	Thompson & Zhao 1993
R. formosensis Kuntze	28	Thompson & Zhao 1993
R. fulvus Focke	14	Subramanian 1987
R. gardnerianus Kuntze	14	Subramanian 1987
R. gardnerianus Kuntze	56	Gill et al. 1984; Singhal et al. 1990
R. glomeratus Blume	98	Borgmann 1964 (No. 200)
R. hakonensis Franch. & Sav.	42	Jinno 1958; Naruhashi & Iwatsubo 1993
R. hakonensis Franch. & Sav.	56	Jinno 1951b, 1958; Naruhashi & Iwatsubo 1993
R. hayata-koidzumii Naruh.	28	Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. calycinoides Hayata var. *macrophyllus* Li	14	Hsu 1968
R. henryi Hemsl. & Kuntze	28	Thompson 1995a
R. hexagynus Roxb.	28	Sarkar et al. 1977
R. hillii F. Muell.	42	Thompson 1995a
R. hunanensis Hand.-Mazz.	28	Thompson 1995a
R. ichangensis Hemsl. & Kuntze	28	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993
R. indicus Thunb.	56	Nybom 1980, 1986
R. irenaeus Focke	42	Thompson & Zhao 1993
R. lambertianus Ser.	28	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993
R. lambertianus Ser. var. *glaber* Hemsl.	28	Thompson 1995a
R. lambertianus Ser. var. *glandulosus* Card.		
R. morii Hayata	28	Hsu 1968
R. mallotifolius Wu ex Yü & Lu	28	Thompson & Zhao 1993
R. micropetalus Gardner	14	Subramanian 1987
R. moluccanus L.	28	Nybom 1986
R. multibracteatus Lév. & Vaniot	28	Thompson & Zhao 1993
R. nesiotes Focke	28	Iwatsubo & Naruhashi 1993
R. paniculatus Sm.	14	Malik 1965; Mehra & Dhawan 1966
R. reflexus Ker	42	Thompson & Zhao 1993
R. rugosus Sm.	14	Malla et al. 1975; Subramanian 1987
R. rugosus Sm.	56	Iwatsubo & Naruhashi 1992
R. rugosus Sm.	98	Nybom 1986

Table 1. Continued.

Taxon	2*n*	References
R. rugosus Sm. var. *thwaitesii* Focke	98	Nybom 1980
R. rugosus Sm. cv. Keriberry	98	Thompson 1995b
R. setchuenensis Bureau & Franch.	28	Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. omeiensis Rolfe	28	Marks 1952
R. sieboldii Blume	28	Jinno 1951a, 1958; Iwatsubo et al. 1992; Iwatsubo & Naruhashi 1992
R. swinhoei Hance	28	Thompson 1995a
R. tephrodes Hance	28	Vaarama 1954; Thompson & Zhao 1993
R. tephrodes Hance var. *ampliflorus* (Lév. & Vaniot) Hand.-Mazz.	28	Thompson 1995a
R. tiliaceus Sm.	28	Iwatsubo & Naruhashi 1993
R. tsangorum Hand.-Mazz.	28	Thompson 1995a
R. xanthoneurus Focke ex Diels	28	Thompson & Zhao 1993
Subgenus *Anoplobatus* Focke		
R. deliciosus Torr.	14	Thompson 1995a
R. deliciosus Torr.	21	Longley 1924
R. neomexicanus A. Gray	14	Thompson 1995a
R. odoratus L.	14	Longley 1924; Yeager & Meader 1958; Wcislo 1987; Thompson 1995a
Rubacer odoratum (L.) Rydb.	14	Löve 1987
R. parviflorus Nutt.	14	Darrow & Longley 1933; Vaarama 1954; Taylor & Mulligan 1968; Thompson 1995a
Rubacer parviflorum (Nutt.) Rydb.	14	Löve 1987
Subgenus *Idaeobatus* Focke		
R. adenophorus Rolfe	14	Longley & Darrow 1924; Thompson & Zhao 1993
R. apetalus Poir.	14	Spies & DuPlessis 1985; Spies et al. 1985
R. apetalus Poir.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. archboldianus Merr. & Perry	ca. 91	Borgmann 1964 (No. 65)
R. biflorus Buch.-Ham. ex Smith	14	Williams et al. 1949; Malik 1965; Mehra & Dhawan 1966
R. chingii Hu	14	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993
R. cockburnianus Hemsl.	14	Thompson & Zhao 1993; Thompson 1995a
R. giraldianus Focke ex Diels	14	Vaarama 1954; Britton & Hull 1957
R. columellaris Tutcher	14	Thompson & Zhao 1993; Thompson 1995a
R. commersonii Poir.	14	Iwatsubo & Naruhashi 1993
R. corchorifolius L.f.	14	Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. coreanus Miq.	14	Longley & Darrow 1924; Williams et al. 1949; Marks 1952; Britton & Hull 1957; Pool et al. 1981; Iwatsubo & Naruhashi 1991; Thompson & Zhao 1993; Thompson 1995a
R. crataegifolius Bunge	14	Vaarama 1954; Keep 1958; Naruhashi 1989; Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. wrightii A. Gray	14	Jinno 1951b, 1958
R. croceacanthus Lév.	14	Iwatsubo & Naruhashi 1992
R. ellipticus Sm.	14	Malik 1965; Mehra & Dhawan 1966; Mehra et al. 1973; Malla et al. 1974; Gill et al. 1984; Subramanian 1987; Singhal et al. 1990; Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. eustephanos Focke ex Diels	14	Thompson 1995a
R. flosculosus Focke	14	Vaarama 1954; Britton & Hull 1957; Thompson & Zhao 1993; Thompson 1995a
R. foliolosus D. Don	14	Malik 1965; Iwatsubo & Naruhashi 1993
R. foliolosus D. Don	28	Malla et al. 1977
R. grayanus Maxim.	14	Iwatsubo & Naruhashi 1993
R. hawaiensis A. Gray	14	Keep 1958; Thompson 1995a
R. hirsutus Thunb.	14	Jinno 1951a, 1958; Naruhashi 1989; Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. hoffmeisterianus Kunth & Bouche	14	Thompson 1995a
R. hypargyrus Edgew. var. *niveus* H. Hara		
R. gracilis Roxb. sensu Focke	14	Marks 1952; Britton & Hull 1957
R. niveus Wall. ex G. Don	14	Malik 1965; Britton & Hull 1957
R. niveus Wall. ex G. Don	28	Mehra et al. 1973
R. pedunculosus D. Don sensu Wall.	14	Britton & Hull 1957
R. idaeopsis Focke	14	Thompson & Zhao 1993
R. idaeus L.	14	Longley & Darrow 1924; Crane & Darlington 1927; Yarnell 1932; Rozanova 1934, 1940; Rohweder 1937; Thomas 1940b; Heslop-Harrison 1953; Einset & Pratt 1954; Larsson 1969; Skalinska et al. 1978; Engelskjon 1979; Pool et al. 1981; Dmitrieva & Parfenov 1985; Thompson 1995a
R. idaeus L. var. *anomalus* Arrh.	14	Vaarama 1939
R. idaeus L. var. *buschii* Rozanova		
R. buschii (Rozanova) Grossh. ex Sinkova	14	Magulaev 1976
R. ikenoensis Lév. & Vaniot	14	Iwatsubo & Naruhashi 1992; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. japonicus Maxim.	14	Jinno 1958
R. illecebrosus Focke	14	Longley 1924; Longley & Darrow 1924; Jinno 1951b, 1958; Thompson 1995a
R. innominatus S. Moore	14	Longley & Darrow 1924; Britton & Hull 1957; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a
R. innominatus S. Moore var. *kuntzeanus* (Hemsl.) L.H. Bailey		
R. kuntzeanus Hemsl.	14	Williams et al. 1949
R. inopertus (Diels) Focke	14	Vaarama 1954; Britton & Hull 1957; Thompson & Zhao 1993
R. kisoensis Nakai	14	Naruhashi 1972
R. lasiostylus Focke	14	Longley & Darrow 1924; Britton & Hull 1957; Thompson & Zhao 1993; Thompson 1995a
R. lasiostylus Focke var. *hubeiensis* T.T. Yü et al.	14	Thompson 1995a
R. leucocarpus Arn.	28	Iwatsubo & Naruhashi 1993
R. leucodermis Douglas ex Torrey & A. Gray	14	Darrow & Longley 1933; Thompson 1995a
R. longipedicellatus (Gust.) C.H. Stirt.	14	Spies & DuPlessis 1985; Spies et al. 1985
R. longipedicellatus (Gust.) C.H. Stirt.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. longipedicellatus (Gust.) C.H. Stirt	35	Spies & DuPlessis 1985; Spies et al. 1985
R. lorentzianus Pulle	126	Borgmann 1964 (No. 48)
R. ludwigii Eckl. & Zeyh.	14	Britton & Hull 1957; Spies & DuPlessis 1985; Spies et al. 1985
R. macilentus Cambess.	14	Malik 1965
R. mcvaughnianus Rzed. & Calderon	14	Thompson 1995a
R. mesogaeus Focke	14	Longley & Darrow 1924; Jinno 1958
R. microphyllus L.f.	14	Iwatsubo & Naruhashi 1992
R. microphyllus L.f. var. *incisus* Koidz.	14	Jinno 1958
R. minusculus Lév. & Vaniot	14	Iwatsubo & Naruhashi 1993; Thompson 1995a
R. montis-wilhelmii P. Royen	14	Borgmann 1964
R. nishimuranus Koidz.	28	Ono 1977; Iwatsubo & Naruhashi 1992
R. niveus Thunb.	14	Thomas 1940b; Britton & Hull 1957; Malik 1965; Mehra & Dhawan 1966; Subramanian 1987; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a
R. albescens Roxb.	14	Britton & Hull 1957
R. lasiocarpus Sm.	14	Vaarama 1954; Malik 1965; Mehra & Dhawan 1966
R. niveus Thunb.	28	Mehra et al. 1973
R. occidentalis L.	14	Longley 1924; Longley & Darrow 1924; Thompson 1995a
R. okinawensis Koidz.	14	Iwatsubo & Naruhashi 1993

Table 1. Continued.

Taxon	2*n*	References
R. palmatus Thunb. ex Murray	14	Iwatsubo & Naruhashi 1992; Thompson 1995a
R. coptophyllus A. Gray	14	Jinno 1958
R. fauriei Lév. & Vaniot	14	Jinno 1951b, 1958
R. palmatoides Kuntze	14	Jinno 1951b, 1958
R. palmatus Thunb. ex Murray var. *coptophyllus* (A. Gray) Kuntze	14	Thompson 1995a
R. parvifolius L.	14	Jinno 1951a, 1958; Williams et al. 1949; Britton & Hull 1957; Bammi 1965b; Probatova et al. 1989; Iwatsubo & Naruhashi 1991; Thompson & Zhao 1993; Thompson 1995a
R. triphyllus Thunb.	14	Longley 1924
R. parvifolius L.	21	Naruhashi & Iwatsubo 1993
R. peltatus Maxim.	14	Jinno 1958; Iwatsubo & Naruhashi 1992
R. phoenicolasius Maxim.	14	Longley & Darrow 1924; Chomisury 1927; Jinno 1951b, 1958; Britton & Hull 1957; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993
R. pinfaensis Lév. & Vaniot	14	Thompson 1995a
R. pinnatus Willd.	14	Spies & DuPlessis 1985; Spies et al. 1985
R. pinnatus Willd.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. probus L.H. Bailey		
R. muelleri F.M. Bailey	28	Thompson 1995a
R. pseudoacer Makino	14	Jinno 1958; Iwatsubo & Naruhashi 1993
R. pungens Cambess.	14	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. racemosus Roxb.	14	Subramanian 1987
R. ribisoideus Matsum.	14	Jinno 1958
R. rosifolius Sm.	14	Thompson & Zhao 1993; Thompson 1995a
R. rosifolius Sm. var. *coronarius* (Sims.) Focke	14	Thompson 1995a
R. sachalinensis Lév.	28	Rozanova 1939; Krogulevich 1976, 1978; Krogulevich & Rostovtseva 1984; Zhukova et al. 1977; Yurtsev & Zhukova 1982; Thompson 1995a
R. idaeus L. var. *melanolasius* Focke (N.E. Asia)	28	Rozanova 1939
R. idaeus L. var. *sachalinensis* (Lév.) Focke (N.E. Asia)	28	Rozanova 1939
R. idaeus L. var. *sibiricus* Kom. (N.E. Asia)	28	Rozanova 1939
R. simplex Focke	14	Vaarama 1954; Iwatsubo & Naruhashi 1993; Thompson & Zhao 1993; Thompson 1995a
R. spectabilis Pursh.	14	Darrow & Longley 1933; Taylor & Mulligan 1968; Iwatsubo & Naruhashi 1992; Thompson 1995a

Table 1. Continued.

Taxon	2*n*	References
R. strigosus Michx.	14	Longley & Darrow 1924; Yarnell 1936; Rozanova 1939; Fischer et al. 1941; Williams et al. 1949; Einset & Pratt 1954; Vaarama 1954; Thompson 1995a
R. idaeus L. var. *canadensis* Richardson	14	Longley 1924
R. idaeus L. var. *melanolasius* Focke (No. Amer.)	14	Löve & Löve 1982a; Packer & Witkus 1982
R. idaeus L. var. *sachalinenesis* (Lev.) Focke (No. Amer.)	14	Löve & Löve 1966
R. idaeus L. var. *strigosus* Michx.	14	Yarnell 1932; Einset & Pratt 1954
R. strigosus Michx.	21	Einset 1947
R. subcrataegifolius (Lév. & Vaniot) Lév. & Vaniot		
R. koehneanus Focke	14	Jinno 1958
R. microphyllus L.f. var. *subcrataegifolius* Lév. & Vaniot	14	Thompson 1995a
R. sumatranus Miq.	14	Iwatsubo & Naruhashi 1992; Thompson & Zhao 1993; Thompson 1995a
R. asper Wall. ex D. Don	14	Jinno 1958
R. thibetanus Franch.	14	Britton & Hull 1957; Thompson & Zhao 1993
R. tokin-ibara Naruh.		
R. commersonii auct. Japon., non Poir	14	Jinno 1951b, 1958
R. eustephanos Focke var. *coronarius* Koidz.	14	Jinno 1958
R. trianthus Focke	14	Thompson & Zhao 1993; Thompson 1995a
R. trifidus Thunb. ex Murray	14	Jinno 1951b, 1958; Iwatsubo & Naruhashi 1992; Thompson 1995a
R. vernus Focke	14	Iwatsubo & Naruhashi 1993
R. xanthocarpus Bureau & Franch.	14	Gustafsson 1933
R. yabei Lév. & Vaniot	14	Jinno 1958
R. yoshinoi Koidz.	14	Naruhashi & Iwatsubo 1993
R. yoshinoi Koidz.	21	Naruhashi & Iwatsubo 1993
Subgenus *Micranthobatus* (Fritsch) Kalkman (= *Lampobatus* sensu Focke pro parte)		
R. cissoides A. Cunn.	28	Thompson 1995a
R. parvus Buchanan	28	Beuzenberg & Hair 1983
R. royenii Kalkman var. *hispidus* Kalkman	28	Borgmann 1964 (No. 203)
R. schmidelioides A. Cunn.	28	Thompson 1995a
R. squarrosus Fritsch	28	Thompson 1995a

Table 1. Continued.

Taxon	2n	References
Subgenus *Rubus* L. (European blackberry species)		
Section *Rubus*		
R. adscitus Genev. subsp. *macrothyrsus* Lange	28	Beijerinck 1956
R. adornatus P.J. Müll.	28	Beijerinck 1956
R. adspersus Weihe ex H.E. Weber	28	Iwatsubo et al. 1995
R. ahenifolius W.C.R. Watson	28	Heslop-Harrison 1953
R. amisiensis H.E. Weber	28	Iwatsubo et al. 1995
R. amplificatus Lees	28	Heslop-Harrison 1953
R. schlechtendalii auct. pro parte, non Weihe ex Link	28	Crane 1935; Fabergé (Maude 1939)
R. anglocandicans A. Newton		
R. falcatus auct.	35	Heslop-Harrison 1953
(as *R. thyrsoideus* sp. coll.)	35	Marks 1952
R. apricus Wimm.	28	Boratynska 1995
R. armeniacus Focke	28	Gustafsson 1943; Thompson 1995a
(as *R. procerus* P.J. Müll. cv. Himalaya)	28	Darrow & Longley 1933; Crane 1935; Berger 1953; Beijerinck 1956; Markarian & Olmo 1959; Haskell 1960; Haskell & Tun 1961; Bammi 1965a; Bammi & Olmo 1966
R. armipotens W.C. Barton ex A. Newton		
R. pseudobifrons (sensu W.C.R. Watson, non Sudre)	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. arrhenii (Lange) Lange	28	Gustafsson 1933, 1939; Beijerinck 1956
R. arrhenii (Lange) Lange var.	28	Heslop-Harrison 1953
R. atrichantherus E.H.L. Krause grex *mucronatus*	28	Gustafsson 1939
R. axillaris Lej.	28	Thompson 1995a
R. scanicus Aresch.	28	Harrison (Maude 1939); Gustafsson 1939, 1943
R. badius Focke	28	Beijerinck 1956
R. bakerianus W.C. Barton & Ridd.	28	Heslop-Harrison 1953
R. bartonii A. Newton cv. Ashton Cross	28	Thompson 1995b
R. bertramii G. Braun	28	Harrison (Maude 1939)
R. bifrons Vest	28	Christen 1950
R. bloxamianus Colemanex Purchas	42	Harrison (Maude 1939)
R. bloxamii (Bab.) Lees	28	Datta 1932
R. boraeanus Genev.	28	Heslop-Harrison 1953
R. bregutiensis A. Kern. ex Focke	28	Christen 1950
R. brevistaminosus Edees & A. Newton		
(as *R. braeuckeri* sensu W.C.R. Watson (1958), non G. Braun)	21	Heslop-Harrison 1953
R. calvatus Lees ex A. Bloxam	28	Haskell 1960

Table 1. Continued.

Taxon	2*n*	References
R. canescens DC.	14	Gilli 1969; Thompson 1995a
R. tomentosus Borkh. pro parte	14	Gustafsson 1933, 1939, 1943; Christen 1950; Berger 1953; Beijerinck 1956; Haskell 1960; Haskell & Tun 1961
R. tomentosus Borkh. var. *glabratus* Godr.	14	Markova 1968
R. cardiophyllus Lefèvre & P. J. Müll.	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. caucasicus Focke	28	Thompson 1995a
R. chaerophyllus Sagorski & W. Schultze var. *chaerophyllus*	28	Beijerinck 1956
R. chloophyllus Sudre (as *R. bertramii* G. Braun)	28	Harrison (Maude 1939)
R. chlorothyrsus Focke	28	Beijerinck 1956
R. chrysoxylon (W.M. Rogers) W.M. Rogers	28	Harrison (Maude 1939)
R. cimbricus Focke	28	Gustafsson 1939
R. cissburiensis W.C. Barton & Ridd. (as *R. separinus* Genev.)	28	Heslop-Harrison 1953
(as *R. separinus* Genev., dwarf form)	28	Heslop-Harrison 1953
R. clusii Borbas *R. gremlii* Focke	28	Gilli 1969
R. conothyrsoides H.E. Weber	28	Iwatsubo et al. 1995; Thompson 1995a
R. crespignyanus W.C.R. Watson	28	Heslop-Harrison 1953
(as *R. calvatus* Lees)	28	Crane 1935
R. cyri Juz.	28	Thompson 1995a
R. dasyphyllus (W.M. Rogers) E.S. Marshall	28	Gustafsson 1939, 1943; Iwatsubo et al. 1995
R. dentatifolius (Briggs) W.C.R. Watson (as *R. uncinatus* P.J. Müll.)	28	Harrison (Maude 1939)
R. distractus P. J. Müll. ex. Wirtg. *R. menkei* Weihe	28	Beijerinck 1956
R. divaricatus P.J. Müll.		
R. nitidus auct., non Weihe & Nees	21	Heslop-Harrison 1953
R. nitidus auct., non Weihe & Nees	28	Datta 1932
R. nitidus Weihe & Nees pro parte	21	Gustafsson 1943; Beijerinck 1956
R. diversus W.C.R. Watson	28	Heslop-Harrison 1953
R. drejeri Jensen ex Lange	28	Gustafsson 1939; Thompson 1995a
R. drejeri Jensen ex Lange	35	Marks 1952
R. dumnoniensis Bab.	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. echinatoides (W.M. Rogers) Dallman	28	Heslop-Harrison 1953
R. echinatus Lindl.		

Table 1. Continued.

Taxon	2*n*	References
R. discerptus P.J. Müll	28	Harrison (Maude 1939)
R. egregius Focke	28	Gustafsson 1939; Heslop-Harrison 1953; Beijerinck 1956
R. elatior Focke ex Gremli	21	Gustafsson 1943
R. elegantispinosus (A. Schumach.) H.E. Weber	28	Iwatsubo et al. 1995
R. errabundus W.C.R. Watson	28	Heslop-Harrison 1953
R. erythrops Edees & A. Newton	28	Thompson 1995a
R. rosaceus sensu W.C.R. Watson, non Weihe	28	Faberge (Maude 1939); Heslop-Harrison 1953
R. fissus Lindl.	21	Beijerinck 1956
R. fissus Lindl.	28	Gustafsson 1939; Heslop-Harrison 1953
R. foliosus Weihe	28	Iwatsubo et al. 1995
R. foliosus Weihe subsp. *flexuosus* P.J. Müll.	28	Beijerinck 1956
R. formidabilis Lefèvre & P.J. Müll.	28	Harrison (Maude 1939)
R. formidabilis Lefèvre & P.J. Müll.	35	Heslop-Harrison 1953
R. furvicolor Focke	28	Heslop-Harrison 1953
(as *R. leyanus* W.M. Rogers)	28	Harrison (Maude 1939)
R. gelertii Frid.	28	Gustafsson 1939; Iwatsubo et al. 1995
R. geniculatus Kaltenb.	28	Beijerinck 1956
R. georgicus Focke	28	Thompson 1995a
R. glandithyrsos G. Braun	28	Iwatsubo et al. 1995
R. glanduliger W.C.R. Watson	28	Heslop-Harrison 1953
R. glandulosus Bellardi	28	Thompson 1995a
R. gliviciensis Sprib.	28	Boratynska 1994
R. godronii Lecoq & Lamotte subsp. *winteri* P.J. Müll.	28	Beijerinck 1956
R. grabowskii Weihe ex Gunther et al.		
R. thyrsanthus Focke	21	Gustafsson 1939, 1943
R. thyrsanthus Focke var. *subvelutinus* Lindeb.		
R. subvelutinus Ripart	21	Gustafsson 1939
R. thyrsoideus Wimm. agg.	21	Longley 1924; Christen 1950
R. gracilis J. & C. Presl	28	Boratynska 1994
R. villicaulis Köhler	28	Beijerinck 1956
R. gratus Focke	28	Fabergé (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956
R. griffithianus W.M. Rogers	28	Heslop-Harrison 1953
R. hartmanii Gand.	28	Thompson 1995a
R. horridus Hartm.	28	Gustafsson 1943
R. hartmanii Gand.	35	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. hastiformis W.C.R. Watson		
R. thyrsiger Bab.	28	Crane & Darlington 1927; Crane 1935; Thomas 1940a
R. heterobelus Sudre	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. hylophilus Ripley ex Genev.		
R. brittonii W.C. Barton & Ridd.	21	Heslop-Harrison 1953
R. hypomalacus Focke	28	Beijerinck 1956; Iwatsubo et al. 1995
R. imbricatus Hort	28	Datta 1932; Heslop-Harrison 1953
R. incurvatus Bab.	28	Datta 1932; Heslop-Harrison 1953
R. infestisepalus Edees & A. Newton		
R. macrothyrsus sensu W.C.R. Watson (1958), non Lange	14	Harrison (Maude 1939)
R. macrothyrsus sensu W.C.R. Watson (1958), non Lange	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. macrothyrsus sensu W.C.R. Watson (1958), non Lange (dwarf form)	28	Heslop-Harrison 1953
R. infestus Weihe ex Boenn.	28	Fabergé (Maude 1939); Heslop-Harrison 1953
R. infestus Weihe ex Boenn.	42	Fabergé (Maude 1939)
R. taenarium Lindeb.	28	Gustafsson 1939
R. insularis F. Aresch.	28	Gustafsson 1933, 1939, 1943; Thompson 1995a
R. insularis Aresch. subsp. *confinus* (LDGB.) F. Aresch.		
R. confinus Lindeb.	28	Gustafsson 1939
R. iricus Rogers		
(as *R. insularis* F. Aresch.)	28	Harrison (Maude 1939)
R. kollundicola Gust.	35	Gustafsson 1939
R. laciniatus Willd.	28	Crane & Darlington 1927; Crane 1935; Heslop-Harrison 1953; Haskell 1960; Bammi 1965a; Bammi & Olmo 1966; Thompson 1995a
R. langei Jensen ex K. Frid. & Gelert	28	Gustafsson 1939
R. largificus W.C.R. Watson	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. lentiginosus Lees	28	Fabergé (Maude 39)
R. lentiginosus Lees	35	Marks 1952
R. lespinassei Clavaud		
R. coutinhi Samp.	28	Marks 1952
R. leucandriformis Edees & A. Newton		
R. leucandrus sensu W.C.R. Watson (1958), non Focke	28	Heslop-Harrison 1953
R. leucandrus Focke	28	Iwatsubo et al. 1995
R. leucostachys Schleich. ex Sm.		
R. leucostachys Sm.	28	Heslop-Harrison 1953
(as *R. lasioclados* Focke var. *angustifolius* W.M. Rogers)	21	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2n	References
R. lindebergii P.J. Müll.	28	Gustafsson 1939; Heslop-Harrison 1953; Iwatsubo et al. 1995
R. lindleyanus Lees	28	Datta 1932; Beijerinck 1956
R. longifrons W.C.R. Watson		
R. longifolius W.C.R. Watson	28	Harrison (Maude 1939)
R. macrophyllus Weihe & Nees	28	Gustafsson 1943; Heslop-Harrison 1953; Beijerinck 1956; Boratynska 1995; Iwatsubo et al. 1995
R. macrophyllus Weihe & Nees var. *megaphyllus* (P.J. Müll.) Sudre	28	Gustafsson 1943
R. marshallii Focke & W.M. Rogers	35	Heslop-Harrison 1953
R. melanodermis Focke	28	Faberge (Maude 1939)
R. mercicus Bagn.	28	Heslop-Harrison 1953
R. milesii A. Newton		
R. spinulifer auct.	28	Heslop-Harrison 1953
R. koehleri auct.	28	Harrison (Maude 1939)
R. koehleri auct.	35	Marks 1952
R. miszczenkoi Juz.	28	Thompson 1995a
R. mollissimus W.M. Rogers	28	Harrison (Maude 1939)
R. montanus Lib. ex Lej.	21	Iwatsubo et al. 1995
R. candicans Weihe ex Rchb.	21	Gustafsson 1939, 1943; Gilli 1969
R. mucronulatus Boreau		
R. mucronatus Bloxam	28	Beijerinck 1956
R. muenteri T. Marsson	28	Iwatsubo et al. 1995
R. scheutzii Lindeb.	28	Gustafsson 1939, 1943
R. murrayi Sudre	28	Heslop-Harrison 1953
R. adornatus auct.	28	Heslop-Harrison 1953
R. naldretti (J.W. White) W.C.R. Watson	28	Heslop-Harrison 1953
R. nemoralis P.J. Müll.	28	Heslop-Harrison 1953; Boratynska 1994
R. selmeri Lindeb.	28	Fabergé (Maude 1939); Gustafsson 1939
R. nemoralis P.J. Müll. var. *microphyllus* (Lindeb.) W.C.R. Watson	28	Heslop-Harrison 1953
R. neomalacus Sudre	28	Heslop-Harrison 1953
R. nessensis Hall	28	Gustafsson 1943; Heslop-Harrison 1953; Beijerinck 1956; Dmitrieva & Parfenov 1985; Boratynska 1995
R. suberectus G. Anderson	28	Gustafsson 1933, 1939; Christen 1950
R. newbouldii Bab.	28	Harrison (Maude 1939)
R. newbridgensis W.C. Barton & Ridd.	28	Heslop-Harrison 1953
R. newbridgensis W.C. Barton & Ridd.	42	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. nitidiformis Sudre		
R. nitidoides W.C.R. Watson	28	Crane 1935; Fabergé (Maude 1939); Thomas 1940a; Heslop-Harrison 1953; Haskell 1960
R. nitidoides W.C.R. Watson	42	Harrison (Maude 1939)
R. oxyanchus Sudre	28	Heslop-Harrison 1953
R. pallidus Weihe	28	Gustafsson 1933, 1939; Heslop-Harrison 1953; Beijerinck 1956
R. patuliformis Sudre	28	Heslop-Harrison 1953
R. pedemontanus Pinkw.	35	Boratynska 1995; Iwatsubo et al. 1995
R. bellardii Weihe & Nees	35	Gustafsson 1933, 1939; Beijerinck 1956
R. bellardii Weihe & Nees	28	Fabergé (Maude 1939)
R. bellardii Weihe	28	Heslop-Harrison 1953; Czapik 1987
R. permundus W.C.R. Watson (as *R. axillaris* P.J. Müll.)	28	Harrison (Maude 1939)
R. phaeocarpus W.C.R. Watson	28	Heslop-Harrison 1953
R. platyacanthus P.J. Müll. & Lefèvre	28	Iwatsubo et al. 1995
R. carpinifolius Weihe	28	Beijerinck 1956
R. carpinifolius auct.	35	Marks 1952
R. plicatus Weihe & Nees	28	Gustafsson 1933, 1939, 1943; Heslop-Harrison 1953; Vaarama 1951; Beijerinck 1956; Boratynska 1995; Thompson 1995a
R. polyanthemus Lindeb.	28	Gustafsson 1933, 1939, 1943; Heslop-Harrison 1953; Beijerinck 1956; Iwatsubo et al. 1995
R. polyanthemus Lindeb. (dwarf form)	28	Heslop-Harrison 1953
R. praecox Bertoloni	28	Iwatsubo et al. 1995
R. prolongatus Boulay & Letendre ex Corb. (as *R. chrysoxylon* W.M. Rogers)	28	Harrison (Maude 1939)
R. pseudopallidus Gust. ex A. Gust. *R. pallidus* Weihe f. *suecius*	28	Gustafsson 1933, 1939
R. pyramidaliformis (Sudre) Ziel.	28	Boratynska 1994
R. pyramidalis Kaltenb.	26–28	Gustafsson 1943
R. pyramidalis Kaltenb.	28	Heslop-Harrison 1953; Beijerinck 1956; Haskell & Tun 1961; Thompson 1995a
R. pyramidalis Kaltenb. var. *parvifolius* Frid. & Gelert	28	Heslop-Harrison 1953
R. pyramidalis Kaltenb. var. *parvifolius* Frid. & Gelert	42	Heslop-Harrison 1953
R. questieri Lefèvre & P.J. Müll.	28	Harrison (Maude 1939)

Table 1. Continued.

Taxon	2*n*	References
R. radula Weihe ex Boenn.	28	Fabergé (Maude 1939); Gustafsson 1933, 1939; Heslop-Harrison 1953; Markova 1972; Boratynska 1994
R. radula Weihe ex Boenn. var. *angustifolius* Lund	28	Gustafsson 1933, 1939
R. radula Weihe ex Boenn. var. *microphyllus* Lindeb.	28	Heslop-Harrison 1953
R. rhombifolius Weihe ex Boenn.	28	Fabergé (Maude 1939); Iwatsubo et al. 1995
R. rosaceus Weihe	28	Beijerinck 1956
R. rotundifolius (Bab.) A. Bloxam	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. rubritinctus W.C.R. Watson		
R. cryptadenes Sudre	28	Fabergé (Maude 1939); Heslop-Harrison 1953
R. rudis Weihe	28	Gustafsson 1939; Berger 1953; Beijerinck 1956
R. rufescens Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. salteri Bab.	28	Fabergé (Maude 1939)
R. sanctus Schreb.	14	Thompson 1995a
R. sanguineus Friv.	14	Markova 1968
R. scaber Weihe	28	Fabergé (Maude 1939); Heslop-Harrison 1953
R. schlechtendalii Weihe	28	Beijerinck 1956
R. schleicheri Weihe ex Tratt. subsp. *schleicheri*	28	Beijerinck 1956
R. schnedleri H.E. Weber	28	Boratynska 1994
R. scidularum A. Beek	28	Beek 1981
R. sciocharis (Sudre) W.C.R. Watson	28	Heslop-Harrison 1953
R. sciaphilus Lange	28	Gustafsson 1939, 1943
R. scissus W.C.R. Watson f. *acicularis* F. Aresch.	28	Heslop-Harrison 1953
R. senticosus Kohler ex Weihe	28	Beijerinck 1956; Iwatsubo et al. 1995
R. montanus Wirtg.	28	Gustafsson 1943
R. septentrionalis W.C.R. Watson		
R. confinis Lindeb.	28	Gustafsson 1939
R. silvaticus Weihe & Nees	28	Heslop-Harrison 1953; Beijerinck 1956; Iwatsubo et al. 1995
R. sprengelii Weihe	28	Datta 1932; Gustafsson 1933, 1939; Harrison (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956
R. subinermoides Druce	28	Heslop-Harrison 1953
R. sulcatus Vest	28	Fabergé (Maude 1939); Gilli 1969
R. sulcatus Vest	±28	Gustafsson 1943
R. tardus W.C.R. Watson	28	Watson (Maude 1939)
R. tereticaulis P.J. Müll. subsp. *derasifolius* Sudre	28	Beijerinck 1956

Table 1. Continued.

Taxon	2*n*	References
R. ulmifolius Schott	14	Crane & Darlington 1927; Gustafsson 1933, 1939; Rozanova 1940; Heslop-Harrison 1953; Beijerinck 1956; Haskell 1960; Haskell & Tun 1961; Thompson 1995a
R. rusticanus Mercier	14	Datta 1932; Crane 1935; Thomas 1940a
R. ulmifolius Schott var. *inermis* (Willd.) Focke	14	Haskell & Tun 1961; Thompson 1995a
R. rusticanus Mercier var. *inermis*	14	Crane & Darlington 1927; Crane 1935
R. inermis Willd. cv. Burbank Thornless	14	Darrow & Longley 1933
R. vestervicensis Gust.	35	Gustafsson 1939, 1943
R. vestitus Weihe	28	Gustafsson 1939, 1943; Christen 1950; Beijerinck 1956
R. vigorosus P.J. Müll. & Wirtg.	28	Iwatsubo et al. 1995
R. affinis Weihe & Nees pro parte	28	Gustafsson 1933, 1939, 1943; Fabergé (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956; Spies & DuPlessis 1985; Spies et al. 1985
R. villicauliformis A. Newton (as *R. villicaulis* Köhler. agg.)	28	Datta 1932
R. winteri P.J. Müll. ex Focke	28	Fabergé (Maude 1939)
R. wolley-dodii (Sudre) W.C.R. Watson	28	Heslop-Harrison 1953
Section *Rubus* (Doubtful determinations and/or taxonomic status)		
R. acutipetalus Lefèvre & P.J. Müll. (as *R. newbouldii* Bab.)	28	Harrison (Maude 1939)
R. adenolobus W.C.R. Watson (nom. nud.)	28	Heslop-Harrison 1953
R. alterniflorus P.J. Müll. & Lefèvre	28	Heslop-Harrison 1953
R. angustifrons Sudre	28	Heslop-Harrison 1953
R. apiculatus Weihe	28	Harrison (Maude 1939); Heslop-Harrison 1953; Beijerinck 1956; Markova 1968
R. apricus Wimm. var. *sparsipilus* W.C.R. Watson (nom. infaustum)	28	Heslop-Harrison 1953
R. aspericaulis Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. axillaris P.J. Müll. (nom. illeg.)	28	Harrison (Maude 1939)
R. caflischii Focke (uncertain determination)	28	Gustafsson 1943
R. chloocladus W.C.R. Watson *R. pubescens* Weihe	28	Gustafsson 1939
R. chlorothyrsus Focke	28	Heslop-Harrison 1953
R. concolor Ley	28	Heslop-Harrison 1953
R. cordifolius Blox.	28	Harrison (Maude 1939)
R. cordifolius Weihe & Nees	35	Gustafsson 1939
R. cuspidiferus (P.J. Müll. & Lefèvre) Boulay (as *R. cuspidifer* P.J. Müll. & Lefèvre)	28	Heslop-Harrison 1953

Table 1. Continued.

Taxon	2*n*	References
R. dasyphylloides (uncertain tax.)	49	Haskell 1960
R. drymophilus P.J. Müll. & Lefèvre	28	Heslop-Harrison 1953
R. fragrans Focke	42	Haskell 1960
R. fruticosus L. agg.	28	Marks 1952; Baquar & Askari 1970
R. fuscoater Weihe	28	Fabergé (Maude 1939)
R. fuscus Weihe	28	Marks 1952; Beijerinck 1956
R. genevierii Boreau	28	Gustafsson 1933, 1939
R. granulatus Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. hirtus Waldst. & Kit. agg.	28	Gustafsson 1933, 1939, 1943; Harrison (Maude 1939); Heslop-Harrison 1953; Boratynska 1995; Thompson 1995a
R. hirtus Waldst. & Kit. subsp. *kaltenbachii* Metsch var. *kaltenbachii*	28	Beijerinck 1956
R. horridisepalus (Sudre) W.C.R. Watson	28	Fabergé (Maude 1939)
R. hystrix Weihe	28	Heslop-Harrison 1953
R. insectifolius Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. insericatus P.J. Müll. ex Wirtg.	28	Heslop-Harrison 1953
R. integribasis P.J. Müll. ex Boulay	42	Heslop-Harrison 1953
R. kaltenbachii Metsch (uncertain tax.)	28	Gustafsson 1933, 1939
R. lejeunei Weihe	35	Heslop-Harrison 1953
R. leptadenes Sudre	28	Heslop-Harrison 1953
R. macrophylloides Genev.	28	Fabergé (Maude 1939)
R. macrostachys P.J. Müll.	28	Gustafsson 1943
R. magnificus P.J. Müll. ex Genev. (garden form)	42	Marks 1952; Heslop-Harrison 1953
as *R. borreri* Bell-Salt. (garden form)	42	Crane 1935; Thomas 1940a
as *R. borreri* Bell-Salt.	28	Fabergé (Maude 1939)
R. melanoxylon P.J. Müll. & Wirtg. (as *R. leyanus* W.M. Rogers)	28	Fabergé (Maude 1939)
R. mercieri Genev. (local biotype)	21	Christen 1950; Berger 1953
R. nitidus Weihe & Nees subsp. *opacus* Focke	28	Datta 1932
R. obcuneatus Lefèvre & P.J. Müll. (as *R. cenomanensis* Sudre)	35	Heslop-Harrison 1953
R. obscurissimus (Sudre) W.C.R. Watson	28	Harrison (Maude 1939)
R. obscurissimus (Sudre) W.C.R. Watson var. *pallidistaminus*	28	Heslop-Harrison 1953
R. obscurissimus (Sudre) W.C.R. Watson var. *pallidistaminus*	28	Harrison (Maude 1939)
R. obscurus Kaltenb.	42	Harrison (Maude 1939)
R. pedatifolius Genev. (uncertain tax.) *R. clethrophilus* P.J. Müll. (= Genev.?)	28	Heslop-Harrison 1953
	28	Gustafsson 1933, 1939

Table 1. Continued.

Taxon	2*n*	References
R. plinthostylus Genev. (as *R. ornatus* Sudre)	28	Harrison (Maude 1939)
R. podophyllus P.J. Müll.	28	Heslop-Harrison 1953
R. pygmaeopsis Focke (as *R. koehleri* Weihe)	28	Harrison (Maude 1939)
R. rhamnifolius Weihe & Nees	21	Gustafsson 1943
R. rivularis P.J. Müll. & Wirtg.	28	Beijerinck 1956; Markova 1968
R. rotundellus Sudre	42	Harrison (Maude 1930)
R. scabrosus P.J. Müll.	35	Heslop-Harrison 1953
R. schleicheri Weihe ex Tratt.	28	Harrison (Maude 1939)
R. schmidelyanus Sudre var. *longiglandulosus* Sudre	35	Heslop-Harrison 1953
R. semipyramidalis Sudre (uncertain tax.)	35	Heslop-Harrison 1953
R. serpens Weihe ex Lej.	28	Beijerinck 1956
R. serpens Weihe ex Lej. & Courtois f. *arenarius*	28	Allander (Gustafsson 1943)
R. silesiacus Weihe	28	Heslop-Harrison 1953
R. sylvicolus Lefèvre & P.J. Müll.	28	Heslop-Harrison 1953
R. thyrsanthus Focke	28	Heslop-Harrison 1953
R. thysiflorus Weihe	28	Weihe (Maude 1939); Heslop-Harrison 1953
R. ulmifolius Schott var. *heteromorphus* (Ripart) Sudre	28	Heslop-Harrison 1953
R. uncinatiformis Sudre *R. uncinatus* P.J. Müll.	28	Harrison (Maude 1939)
R. vallisparsus Sudre	28	Harrison (Maude 1939); Heslop-Harrison 1953
R. vulgaris Weihe & Nees var. *mollis* Weihe & Nees	21	Heslop-Harrison 1953
Section *Corylifolii* Lindl.		
R. adenoleucus Chab.	35	Heslop-Harrison 1953
R. aureolus Allander	28	Allander 1941; Gustafsson 1943
R. aureolus Allander f. *suberiocarpus* Gust.	28	Gustafsson 1943
R. aureolus Allander var. *subglandulosus* A.A.W. Lund	28	Gustafsson 1943
R. nemorosus sensu Arrh., non Hayne & Willd.	28	Gustafsson 1933, 1939
R. nemorosus sensu Arrh. var. *suberiocarpus* ad int.	28	Gustafsson 1939
R. nemorosus sensu Arrh. var. *subglandulosus* Lund	28	Gustafsson 1939
R. babingtonianus W.C.R. Watson	28	Heslop-Harrison 1953
R. britannicus W.M. Rogers	42	Heslop-Harrison 1953
R. calvus H.E. Weber	28	Iwatsubo et al. 1995

Table 1. Continued.

Taxon	2*n*	References
R. camptostachys G. Braun		
R. divergens Neuman	42	Gustafsson 1933
R. ciliatus Lindeb.	28	Gustafsson 1939
R. ciliatus Lindeb.	±30	Gustafsson 1939
R. ciliatus Lindeb. var. *tiliaceus* (Aresch.) Gust.	28	Gustafsson 1943 (erroneously given as 42 in Gustafsson 1939)
R. conjungens (Bab.) W.M. Rogers	28	Heslop-Harrison 1953
R. conjungens (Bab.) W.M. Rogers	35	Heslop-Harrison 1953
R. purpureicaulis W.C.R. Watson	35	Heslop-Harrison 1953
R. contractipes H.E. Weber	28	Iwatsubo et al. 1995
R. cyclomorphus H.E. Weber		
R. cyclophyllus Lindeb.	42	Gustafsson 1939
R. demissus H.E. Weber & Martensen	28	Iwatsubo et al. 1995
R. dissimulans Lindeb. var. *bahusiensis* (Scheutz) Gust.	28	Gustafsson 1943 (erroneously given as 42 in Gustafsson 1933)
R. dissimulans Lindeb. var. *selectus* Frid.	42	Gustafsson 1939, 1943
R. dissimulans Lindeb. var. *suberectiformis* (Neuman) Gust.	28	Gustafsson 1939
R. dissimulans Lindeb. f. *ferox* (Frid.) Erichsen		
R. ferox Frid.	±42	Gustafsson 1939
R. nitens (Lindeb.) Neuman	42	Gustafsson 1933
R. dollnensis Sprib.	28	Boratynska 1994
R. eluxatus Neuman	28	Gustafsson 1943
R. centiformis Frid. pro parte	28	Gustafsson 1939
R. eluxatus Neuman ad *subnitidus* vergens	±28	Gustafsson 1939
R. eluxatus Neuman f. *subnitidus* Lidf.	28	Gustafsson 1939
R. eluxatus Neuman f. *subnitidus* Lidf.	45	Gustafsson 1933
R. fasciculatus P.J. Müll.	42	Gustafsson 1939
R. ambifarius P.J. Müll.	28	Gustafsson 1939, 1943
R. ambifarius P.J. Müll.	35	Gustafsson 1939
R. permixtus (Aresch.) A. Gust.	28	Gustafsson 1939
R. permixtus (Aresch.) A. Gust.	28–29	Gustafsson 1943
R. ferocior H.E. Weber	28	Iwatsubo et al. 1995
R. fioniae Frid. ex Neuman	28	Gustafsson 1939
R. glauciformis Gust. ex H. Hyl.	28	Gustafsson 1943
(*R. caesius* × *wahlbergii*) f. *glauciformis* Gust.	28	Gustafsson 1939

Table 1. Continued.

Taxon	2*n*	References
R. gothicus Frid. & Gelert ex E.H.L. Krause	28	Gustafsson 1939, 1943
R. gothicus Frid. & Gelert ex E.H.L. Krause	±28	Gustafsson 1939
R. acuminatus Lindeb.	28	Gustafsson 1933
R. gothicus Frid. & Gelert ex E.H.L. Krause	35	Gustafsson 1939
R. gothicus Frid. & Gelert ex E.H.L. Krause f. *microphylla*	28	Gustafsson 1939
R. gothicus Frid. & Gelert ex E.H.L. Krause f. *umbrosa*	28	Gustafsson 1943
R. grossus H.E. Weber	35	Boratynska 1994
R. hallandicus (Gabr. ex Aresch.) Neuman	28	Gustafsson 1939, 1943
R. halsteadensis W.C.R. Watson		
R. raduliformis (Ley) W.C.R. Watson	35	Heslop-Harrison 1953
R. hystricopsis (Frid.) A. Gust.	28	Gustafsson 1939
R. lagerbergii Lindeb.	35	Gustafsson 1943
R. lamprocaulos G. Braun	28	Iwatsubo et al. 1995
R. serrulatus Lindeb. f. *eglandulosa* Gust.	28	Gustafsson 1943
R. serrulatus Lindeb. f. *ditior* Frid.	28	Gustafsson 1939
R. lidforssii (Gelert) Lange		
R. centiformis var. *lidforssii* (Gelert) A. Gust.	28–35	Gustafsson 1939
R. centiformis var. *lidforssii* (Gelert) A. Gust.	28	Gustafsson 1939
R. lindbloomii Westerl.		
R. centiformis Frid. var. *mortensenii* Frid. & Gelert	28	Gustafsson 1939
R. centiformis Frid. var. *mortensenii* Frid. & Gelert	42	Gustafsson 1939
R. nemorosus Hayne & Willd.	28	Iwatsubo et al. 1995
R. balfourianus A. Bloxam ex Bab.	28	Heslop-Harrison 1953
R. balfourianus A. Bloxam ex Bab.	35	Heslop-Harrison 1953
R. norvegicus H.E. Weber & Pedersen		
R. rosanthus Lindeb. var. *lejocarpus* Lindeb.	28	Gustafsson 1939, 1943
R. rosanthus Lindeb. var. *lejocarpus* Lindeb.	35	Gustafsson 1943
R. rosanthus Lindeb. var. *lejocarpus* Lindeb.	49	Gustafsson 1939
R. orthostachys G. Braun	28	Boratynska 1994
R. phylloglota (Frid.) A. Gust.	28	Gustafsson 1939
R. pruinosus Arrh. f. *pruinosus*	35	Gustafsson 1939
R. sublustris Lees	35	Heslop-Harrison 1953
R. pruinosus Arrh. var. *silvaticus* Gust. ad int.	35	Gustafsson 1939
R. pruinosus Arrh. f. *warmingii* (Jensen ex Neuman) H.E. Weber		
R. pruinosus Arrh. var. *opimus* A.A.W. Lund	35	Gustafsson 1943
R. pruinosus Arrh. var. *warmingii* (Jensen ex Neuman) Gust. ex A. Gust.	35	Gustafsson 1939, 1943

Table 1. Continued.

Taxon	2*n*	References
R. rhytidophyllus H.E. Weber	28	Iwatsubo et al. 1995
R. rosanthus Lindeb. var. *eriocarpus* Lindeb.	35	Gustafsson 1939
R. slesvicensis Lange	42	Thompson 1995a
R. suecius H.E. Weber & Karlsson		
R. fioniae Frid. var. *benefixus* Gust.	28	Gustafsson 1943
R. tiliaster H.E. Weber		
R. tileaceus Lange	42	Gustafsson 1933
R. tuberculatus Bab.	35	Heslop-Harrison 1953
R. myriacanthus auct.	35	Heslop-Harrison 1953
R. wahlbergii Arrh.	35	Gustafsson 1939, 1943; Thompson 1995a
R. wahlbergii Arrh. var. *magnificus* Frid.	35	Gustafsson 1939
R. wahlbergii Arrh. var. *partitus* Gust.	35	Gustafsson 1939
R. wahlbergii Arrh. f. *umbrosa*	35	Gustafsson 1939
R. insulariformis (local form of walhlbergii?)	42	Gustafsson 1933
R. warrenii Sudre	28	Heslop-Harrison 1953
Section *Corylifolii* (Doubtful determinations and/or taxonomic status)		
R. acutus Lindeb. nom. illeg.; non *acutus* Braeucker	42	Gustafsson 1939
R. acutus Lindeb. var. *fioniaeformis* Newman	28	Gustafsson 1943
R. acutus Lindeb. var. *nemorosiformis* Neuman	28	Gustafsson 1943
R. acutus Lindeb. var. *ruedensis* (Lidf.)	42	Gustafsson 1939
R. acutus Lindeb. var. *progenerans* (Lidf.)?	42	Gustafsson 1939
R. adenoleucus Chab.	35	Heslop-Harrison 1953
R. corylifolius Sm. agg.	28	Longley 1924
R. corylifolius Sm. agg.	35	Datta 1932
R. dumetorum Weihe	35	Marks 1952
R. galbidus Kan.	28	Gustafsson 1943
R. internatus Gust. ex H. Hyl.		
R. ruderalis Aresch. (local biotype)	±30	Gustafsson 1939
R. maximus (L. ex Aresch.) Neuman, non *maximus* T. Marsson (nom. illeg.-local biotype)		
R. balticus Aresch.	49	Gustafsson 1939
R. lagerbergii Lindeb. var. *balticus* Aresch.	49	Gustafsson 1933
R. lagerbergii Lindeb. var. *balticus* (Aresch.) Frid.	35/2	Gustafsson 1943
R. lagerbergii Lindeb. var. *balticus* (Aresch.) Frid.	70?	Gustafsson 1943 (given as $n = 35$)
R. ostenfeldii Frid. (vars. represent limited local forms)		
R. ostenfeldii Frid. var. *micrander* Frid.	28	Gustafsson 1939
R. ostenfeldii Frid. var. versus *warmingii*	42	Gustafsson 1939

Table 1. *Continued.*

Taxon	2*n*	References
R. ostenfeldii Frid. var. versus *warmingii*	±44	Gustafsson 1939
R. olavii Neuman f. (invalid name)	±42	Gustafsson 1939
R. rotundellus Sudre	42	Harrison (Maude 1939)
R. scabrosus Focke	35	Heslop-Harrison 1953
R. trivultus Frid. f. *kullensis*	28	Gustafsson 1933
R. umbelliformis P.J. Müll. & Lefèvre	35	Heslop-Harrison 1953
R. vexatus Frid. (local biotype)		
R. vexatus Frid. var. *crispus* Frid.	42	Gustafsson 1939
Section *Caesii* Lej. & Courtois		
R. caesius L.	28	Longley 1924; Datta 1932; Gustafsson 1933, 1939, 1943; Rozanova 1934, 1940; Rohweder 1937; Vaarama 1939; Christen 1950; Berger 1953; Beijerinck 1956; Haskell 1960; Haskell & Tun 1961; Engelskjon 1979; Boratynska 1995; Thompson 1995a
R. caesius L. var. *turkestanicus* Regel	28	Longley 1924; Rozanova 1934, 1940
Subgenus *Rubus* (North American blackberry species)		
Section *Allegheniensis*		
R. allegheniensis Porter	14	Longley 1924; Einset 1947; Einset & Pratt 1954; Aalders & Hall 1966
R. villosus American authors non Aiton	14	Longley 1924
R. allegheniensis Porter	21	Longley 1924; Einset 1947
R. avipes L.H. Bailey	21	Einset 1947
R. pergratus Blanch.	21	Longley 1924
R. sativus Brainerd (pro parte)	21	Longley 1924
R. alumnus L.H. Bailey		
R. bellobatus L.H. Bailey	21	Einset 1947
R. bellobatus L.H. Bailey	28	Einset 1947
R. pugnax L.H. Bailey	14	Einset 1947
R. rosa L.H. Bailey	21	Einset 1947
Section *Arguti*		
R. abactus L.H. Bailey	35	Einset 1947
R. amnicolus Blanch.	21	Longley 1924
R. andrewsianus Blanch.	21	Longley 1924
R. argutus Link	14	Longley 1924
R. argutus Link	21	Longley 1924
R. floridus Tratt. cv. Early Harvest	14	Fischer et al. 1941

Table 1. Continued.

Taxon	2*n*	References
R. frondosus Bigelow	14	Longley 1924
R. frondosus Bigelow	21	Longley 1924
R. frondosus Bigelow	42	Longley 1924
R. louisianus A. Berger	14	Markarian & Olmo 1959
R. orarius Blanch.	21	Longley 1924
R. pensilvanicus Poir.	28	Einset 1947
R. recurvans Blanch.	21	Longley 1924
R. cardianus L.H. Bailey (syn.?)	35	Einset 1947
R. recurvans Blanch.		
R. wiegandii L.H. Bailey	36	Einset 1947
R. recurvans Blanch.	42	Longley 1924
R. uniquus L.H. Bailey	28	Einset 1947
R. uvidus L.H. Bailey		
R. localis L.H. Bailey	21	Einset 1947
Section *Canadenses*		
R. canadensis L.	14	Longley 1924; Thompson 1995a
R. randii Rydb.	14	Longley 1924
R. canadensis L.	21	Longley 1924; Einset 1947; Craig 1960; Thompson 1995a
Section *Cuneifolii*		
R. cuneifolius Pursh	14	Sharpe & Shoemaker 1958; Shoemaker & Sturrock 1959; Sherman 1968; Spies & DuPlessis 1985; Spies et al. 1985
R. cuneifolius Pursh	21	Spies & DuPlessis 1985; Spies et al. 1985
R. cuneifolius Pursh	28	Spies & DuPlessis 1985; Spies et al. 1985
R. pascuus L.H. Bailey	21	Spies & DuPlessis 1985; Spies et al. 1985
R. pascuus L.H. Bailey	28	Spies & DuPlessis 1985; Spies et al. 1985
R. serissimus L.H. Bailey	28	Einset 1947
Section *Flagellares*		
R. aboriginum Rydb. cvs. Austin Dew, Austin Thornless, and Austin Mayes	56	Thompson 1961
R. arundelanus Blanch.	42	Longley 1924
R. jeckylanus Blanch.	42	Longley 1924
R. biformispinus Blanch.	21	Longley 1924
R. flagellaris Willd.	28	Spies & DuPlessis 1985; Spies et al. 1985
R. villosus Aiton	35	Longley 1924
R. geophilus Blanchard	49	Einset 1951
R. flagellaris Willd.	56	Faasen & Nadeau 1976

Table 1. Continued.

Taxon	2*n*	References
R. flagellaris Willd.	63	Einset 1947
R. meracus L.H. Bailey	49	Einset 1947
R. multiformis Blanch.	21	Longley 1924
R. noveboracus L.H. Bailey	35	Einset 1947
R. plicatifolius Blanch.	35	Longley 1924
R. plicatifolius Blanch, *R. semierectus* Blanch.	42	Longley 1924
R. recurvicaulis Blanch.	14	Longley 1924
R. roribaccus (L.H. Bailey) Rydb. (as *R. flagellaris*, in part, cv. Lucretia)	49	Thompson 1961
R. satis L.H. Bailey (as *R. plicatifolius* Blanch.)	63	Einset 1947
Section *Hispidi*		
R. hispidus L.	14	Aalders & Hall 1966; Thompson 1995a
R. hispidus L.	35	Longley 1924
R. hispidus-like	56	Longley 1924
R. huttonii L.H. Bailey	28	Einset 1947
R. plus L.H. Bailey	21	Einset 1947
R. signatus L.H. Bailey	21	Einset 1947
R. tardatus Blanch.	21	Longley 1924
Section *Setosi*		
R. clandestinus L.H. Bailey *R. jejunus* L.H. Bailey	28	Einset 1947
R. dissensus L.H. Bailey	21	Einset 1947
R. glandicaulis Blanch.	21	Longley 1924
R. hanesii L.H. Bailey	28	Einset 1947
R. miscix L.H. Bailey *R. peculiaris* Blanch.	21	Longley 1924
R. notatus L.H. Bailey *R. bootianus* L.H. Bailey	14	Einset 1947
R. setosus Bigelow	14	Longley 1924
R. setosus Bigelow	21	Longley 1924
R. nigricans Rydb.	21	Longley 1924

Table 1. Continued.

Taxon	2*n*	References
R. wisconsinensis L.H. Bailey		
R. minnesotanus L.H. Bailey	35	Einset 1947
Section *Verotriviales*		
R. trivialis Michx.	14	Yarnell 1936; Sharpe & Shoemaker 1958; Shoemaker & Sturrock 1959; Sherman 1968; Thompson 1995a, b
R. rubrisetus Rydb.	14	Yarnell 1932
Section *Ursini*		
R. ursinus Cham. & Schltdl.	42	Fischer et al. 1941; Brown 1943; Vaarama 1953
R. loganobaccus L.H. Bailey	42	Darrow & Longley 1933; Thomas 1940a, b; Vaarama 1953
R. ursinus Cham. & Schltdl.	56	Darrow & Longley 1933; Fischer et al. 1941; Brown 1943; Zielinski & Galey 1951; Vaarama 1953; Thompson 1961; Thompson 1995b
R. vitifolius Cham. & Schltdl.	56	Thomas 1940a, b
R. ursinus Cham. & Schltdl.	63	Brown 1943
R. ursinus Cham. & Schltdl.	70	Darrow & Longley 1933; Brown 1943; Vaarama 1953; Thompson 1961
R. ursinus Cham. & Schltdl.	77	Brown 1943
R. ursinus Cham. & Schltdl.	84	Darrow & Longley 1933; Fischer et al. 1941; Brown 1943; Gustafsson 1943; Iwatsubo & Naruhashi 1993; Thompson 1995a, b
R. macropetalus Douglas	84	Darrow & Longley 1933; Zielinski & Galey 1951
Subgenus *Rubus* (South American blackberry species)		
Section *Floribundi*		
R. adenotrichos Schltdl.	14	Thompson 1995a
R. bogotensis Kunth	14	Gustafsson 1939; Dale & Ingram 1981
R. robustus C. Presl	14	Thompson 1995a
R. uticifolius Poir.	14	Thompson 1995a
Proposed Natural Inter-Subgeneric Hybrid		
R. glaucus Benth. (*Rubus* × *Idaeobatus* ?)	28	Williams et al. 1949; Dale & Ingram 1981; Thompson 1995a

NOTICE

THE 1996 JESSE M. GREENMAN AWARD

The 1996 Jesse M. Greenman Award has been won by Paul Kores for his publication "A systematic study of the genus *Acianthus* (Orchidaceae: Diurideae)," published in Allertonia 7: 87–220 (1995). This study is based on a Ph.D. dissertation from Tulane University under the direction of Dr. Steven P. Darwin.

The Greenman Award, a certificate and a cash prize of $1,000, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1996 are now being accepted for the 29th annual award, which will be presented in the summer of 1997. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1996 award, reprints must be received by 1 June 1997.

Volume 84, Number 1, pp. 1–166 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN
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Experimental and Molecular Approaches to Plant Biosystematics

The proceedings of the Fifth International Symposium of the International Organization of Plant Biosystematists (IOPB)

Edited by Peter C. Hoch and A. G. Stephenson

Twenty-three original contributions that span the breadth of biosystematics, a dynamic field of study that bridges the realms of systematics and population biology. The papers are arranged in four groups, reflecting the original four symposia of the 1992 meeting. *DNA and Plant Biosystematics* presents innovative work that uses the rapidly developing nucleic acid methods adapted from molecular biology. *Plant Growth Patterns and Biosystematics* includes comparative and developmental analyses of plant architecture and branching patterns. *Plant Reproductive Strategies* surveys new approaches in the analysis of plant reproductive biology, an area central to both systematic and population-level studies. *Phylogenetic Analysis and Population Biology* emphasizes the application of the powerful new methods of phylogenetic analysis to problems at the species and population levels. Monographs in Systematic Botany from the Missouri Botanical Garden, Volume 53. ISBN: 0-915279-30-4. 416 pp. Illustrated. 1995. $60.00 U.S. $62.00 Non-U.S.

Annals of the Missouri Botanical Garden, Volume 82, Number 2: Alternative Genes for Phylogenetic Reconstruction in Plants

A symposium cosponsored by the American Society of Plant Taxonomists and the Botanical Society of America, organized by Pamela S. Soltis and Douglas E. Soltis, and presented at the 1993 AIBS meetings.

Although the chloroplast gene *rbc*L has been successfully used to reconstruct plant phylogeny, many important questions of plant phylogeny and evolution cannot be addressed using it. The contributors to this issue of the *Annals* explore the potential of eight alternative genes or DNA regions for phylogenetic reconstruction at a variety of hierarchical levels. Both nuclear and chloroplast genes are evaluated. Three regions of the nuclear ribosomal RNA cistron are explored: the 18S gene, the internal transcribed spacers (ITS), and the 26S gene. Small multigene families from the nuclear genome may also carry phylogenetic signal: the phytochrome gene family and the small heat shock gene family. Three genes from the chloroplast genome are also considered: *atp*B, *ndh*F, and *mat*K. Each paper describes the location, size, structure, and rate of evolution of the chosen gene and discusses its potential for phylogenetic study. This issue also contains: "The Comparative Pollination and Floral Biology of Baobabs (*Adansonia*–Bombacaceae)" by David A. Baum and "In Memoriam: *Peter G. Martin.*" Annals 82(2) 1995. 174 pages. $27.50 U.S. $28.00 Non-U.S.

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CONTENTS

Angiosperm Phylogeny Inferred from 18S Ribosomal DNA Sequences ..... *Douglas E. Soltis, Pamela S. Soltis, Daniel L. Nickrent, Leigh A. Johnson, William J. Hahn, Sara B. Hoot, Jennifer A. Sweere, Robert K. Kuzoff, Kathleen A. Kron, Mark W. Chase, Susan M. Swensen, Elizabeth A. Zimmer, Shu-Miaw Chaw, Lynn J. Gillespie, W. John Kress & Kenneth J. Sytsma* 1

Tribal Relationships in the Gesneriaceae: Evidence from DNA Sequences of the Chloroplast Gene *ndh*F ..... *J. F. Smith, J. C. Wolfram, K. D. Brown, C. L. Carroll & D. S. Denton* 50

A Phylogenetic Conspectus of the Tribe Juanulloeae (Solanaceae) ..... *Sandra Knapp, Viveca Persson & Stephen Blackmore* 67

A Revision of the Genus *Xiphotheca* (Fabaceae) ..... *Anne Lise Schutte* 90

A Review of the Genus *Eccremocarpus* (Bignoniaceae) ..... *William G. D'Arcy* 103

Hot-Spots Analysis for Conservation of Plant Biodiversity in the Mediterranean Basin ..... *Frédéric Médail & Pierre Quézel* 112

Survey of Chromosome Numbers in *Rubus* (Rosaceae: Rosoideae) ..... *Maxine M. Thompson* 128

Notice 165

Cover illustration. *Eccremocarpus viridis* Ruiz & Pavón, by Phyllis Bick.

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THE GENUS *LYCIANTHES* (SOLANACEAE) IN VENEZUELA[1]

Carmen Benítez de Rojas[2] *and William G. D'Arcy*[3]

ABSTRACT

The 11 species of *Lycianthes* that occur in Venezuela are described and distinguished with illustrations, a dichotomous key, and notes on their appearance and ranges. The separation of *Lycianthes* from *Solanum* and its closer relationship to *Capsicum* are reviewed in light of morphological and recent molecular evidence.

The genus *Lycianthes* (Dunal) Hassl. includes 150–200 species of herbs and shrubs that range throughout the Neotropics and in southeast Asia. A few species have marketable fruits, and one species is sometimes grown as an ornamental, but otherwise the genus is largely unnoticed. This paper reviews characteristics of the genus *Lycianthes* and revises the species that occur in Venezuela. Photographs of some of these plants are presented in Figure 1. Salient features of the flowers of the Venezuelan species are shown in Figure 2.

Lycianthes was long included in the large genus *Solanum*,which is similar in its flowers and fruits and also in its poricidal anthers. *Solanum lycioides* L., a species with seeds enclosed in sclerenchyma, was separated as the genus *Lycianthes* by Hassler in 1917. Soon after, *Lycianthes* was monographed by Georg Bitter (1920) who expanded the genus to over 100 species, including many lacking sclerenchyma in the fruit. Acceptance of the genus has been hesitant, but most botanists now recognize it as distinct from *Solanum*. D'Arcy (1986) studied the calyx in *Lycianthes*, *Capsicum*, and other relatives and concluded that the unusual calyx warrants generic recognition. He supported Bitter's view that *Lycianthes* is more closely related to *Capsicum* than to *Solanum*. This was accepted by Barboza and Hunziker (1992), Dean (1995), and others. More recently, a classification of the Solanaceae based on chloroplast DNA (Olmstead et al., in press) has

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[2] Facultad Agronomía, Universidad Central de Venezuela, Maracay, Apartado Correos 4597, Aragua, Venezuela.
[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

Figure 1. Selected *Lycianthes* species. A, B. *Lycianthes pauciflora.*—A. Fruits and calyx.—B. Fruiting calyx.—C. *Lycianthes asarifolia.* Flowers and foliage.—D. *Lycianthes pauciflora.* Seeds.—E. *Lycianthes lycioides.* Pyrenes. A, B. After *Benítez & D'Arcy 3271* (MO, MY). C. After *D'Arcy 16261* (MO). D. After *Benítez et al. 5148* (MY). E. After *Nee 17760* (MO).

supported the separation of *Lycianthes* from *Solanum* and placed it near *Capsicum.*

Stone Cells

Some solanaceous fruits contain sclerenchyma in the form of stone cells or sclerocytes, which commonly do not enclose the seed. These are aggregates of secondarily hardened parenchyma cells or sclereids. Bitter (1911, 1914) examined many Solanaceae, and he found them in various berries of *Lycianthes, Solanum,* and other genera of subfamily Solanoideae. He hypothesized that they might be relics from hard walls of ancestrally capsular fruits. Danert (1969) used electron microscopy to examine their genesis in *Solanum.* Stone cells have been used in the Solanaceae as taxonomic clues (Schilling, 1981), but there is still poor confirmation of their constancy in taxa of different levels. They may be diagnostic in some *Lycianthes* taxa, notably *L. lycioides,* but are variable in others, such as *L. pauciflora.* Their presence or absence was noted by Bitter, Barboza and Hunziker (1992), and Dean (1995) in their species descriptions.

The Calyx

In bud, the calyx in *Lycianthes* and *Capsicum* is fused to the top (complete prefloration), and the corolla, stamens, and other interior parts egress from it by a stretching of the calyx apex. This results in a truncate margin subtended by a thin sleeve of tissue with reduced vasculature. Low in the calyx, the five principal calyx traces each diverge into three traces, much as in a foliage leaf, and the adjacent lateral traces are fused together, resulting in a calyx with 10 nerves. Of these, 5 primary ones are produced by the continuation of the principal calyx traces, and 5 are produced secondarily by fusion of the adjacent lateral traces. In

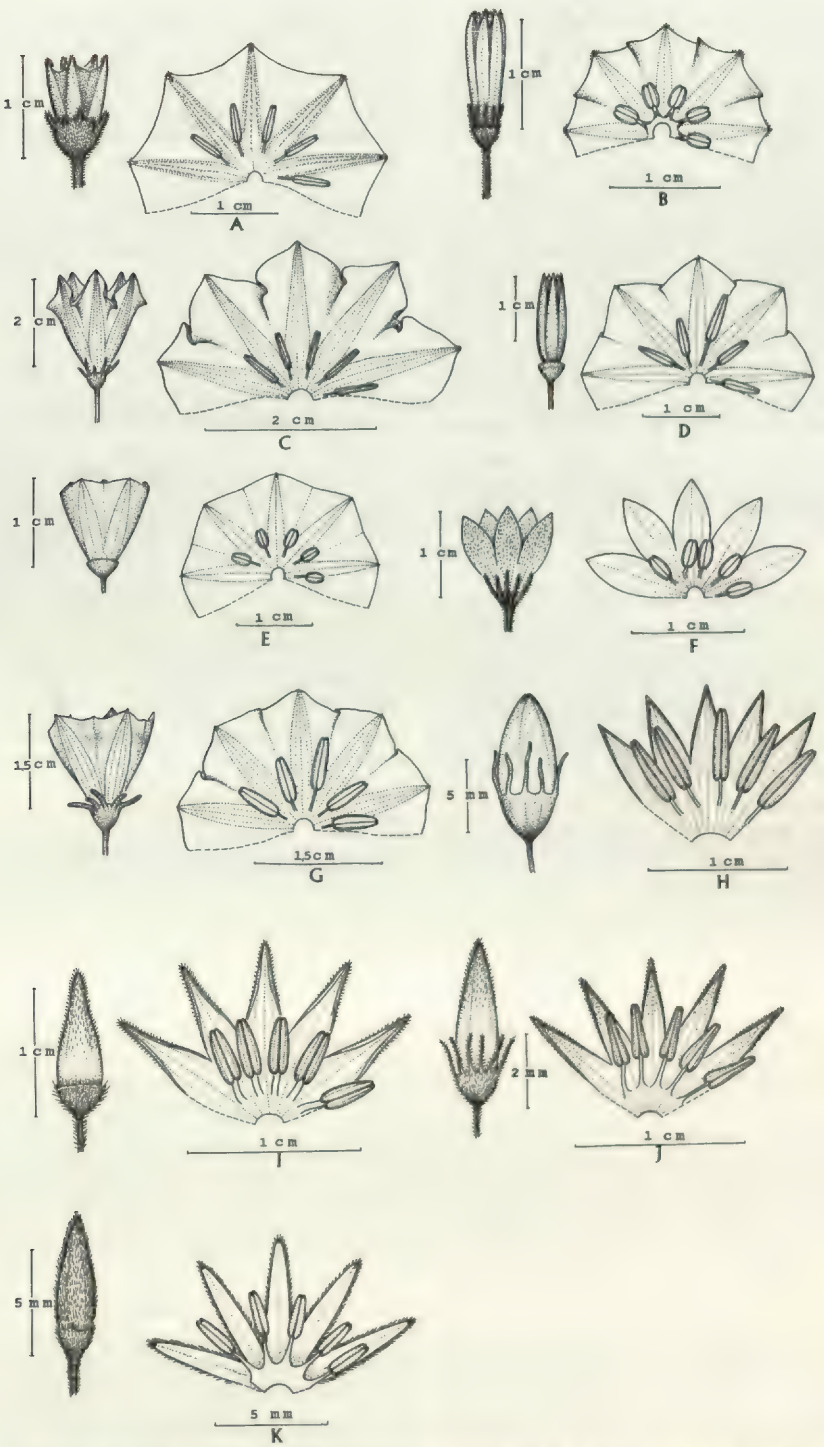

Figure 2. Closed and open flowers of Venezuelan species of *Lycianthes*. Left figure: closed floral buds showing the calyx. Right figure: open flower showing corolla lobing and relative size of stamens.—A. *Lycianthes ferruginea*.—B. *Lycianthes lycioides*.—C. *Lycianthes lenta*.—D. *Lycianthes sanctaemarthae*.—E. *Lycianthes asarifolia*.—F. *Lycianthes acutifolia*.—G. *Lycianthes pauciflora*.—H. *Lycianthes stenoloba*.—I. *Lycianthes inaequilatera*.—J. *Lycianthes amatitlanensis*.—K. *Lycianthes radiata*. A. After *Morillo 6057* (VEN); B. After *Ruíz-Terán 12533* (MY); C. After *Bunting 4433* (MY); D. After *Steyermark 122959* (MO); E. After *Liesner et al. 7803* (VEN); F. After *Ruíz-Terán 64* (MERF); G. After *Ferrari 733* (MY); H. After *Mocquerys 978* (VEN); I. After *Davidse 18899* (VEN); J. After *Steyermark 121528* (VEN); K. After *Steyermark 56628* (MY).

many cases, some or all of these 10 traces enate or bend outward to form umbos or teeth laterally on side of the calyx and below the apical sleeve area. Thus, in *Lycianthes* calyces, all teeth or umbos are lateral and arise below the calyx apex, and no primary teeth are found at the top of the calyx. These structures are shown in Figure 2, and their vasculature was illustrated by D'Arcy (1986).

The extent of lateral vein enation is variable, differing in different species, sometimes in different flowers on the same plant, and sometimes in different veins on the same flower. In different species, there may be no teeth at all or any number from 1 to 10. When there are 10 teeth, they often form two series, the 5 teeth arising from the primary traces larger than those arising from the fused lateral traces. In *Solanum*, calyces have as many teeth as corolla lobes or stamens, usually 5, rarely 4 or 6. Having 4–6 calyx teeth is quite unusual in *Lycianthes*.

The calyx in *Lycianthes*, thus, has three features, thought to be specializations, that are not found in the calyx of *Solanum*: (1) complete prefloration and egress of interior parts by stretching rather than bending out and tearing, which produces an entire, thinned, apical sleeve; (2) fused adjacent lateral traces of the ancestral lobes; and (3) enation of the traces in many species to produce umbos or teeth. However, because they are so alike in other ways, *Solanum* and *Lycianthes* are assumed be derived from a closely related ancestor.

Whether *Solanum* and *Lycianthes* arose independently from a common ancestor or *Lycianthes* arose from within *Solanum* is not revealed in morphological studies of the calyx. The trees used by Olmstead et al. (in press) to illustrate their classification of the Solanaceae depict one clade leading to two phylads (*Lycianthes/Capsicum* and *Solanum/Jaltomata*), each with taxa displaying both porose and longitudinal anther dehiscence. All the porose-dehiscent Solanaceae except the enigmatic *Triguera* of Gibraltar and nearby areas are thus contained in this single clade, and the question remains whether porose dehiscence was derived twice within the clade or was derived once and lost twice.

In *Capsicum*, although calyx prefloration is complete and egress of the interior parts is by stretching as in *Lycianthes*, the sleeve is smaller and less evident, and the lateral traces do not fuse and do not enate to produce secondary umbos or teeth. Thus, *Capsicum* has only two of the three specializations noted above for *Lycianthes*: the complete prefloration and stretching egress of the floral parts, and the enation of primary traces to produce teeth. The fusion of adjacent lateral veins and enation of a second series of teeth is hardly indicated or not present at all. *Capsicum* calyces have 5 teeth; *Lycianthes* calyces seldom have 5 teeth, they usually develop either 10 teeth or fewer than 5.

In his morphological study, D'Arcy (1986) suggested that floral parts in *Witheringia* have a basically similar way of egressing from the calyx and that this genus is probably closely related to the *Lycianthes/Capsicum* group, but the recent study of Olmstead et al. (in press) gives a more distant placement.

Other Characters

Other characters are also useful for recognizing *Lycianthes*, although they are not diagnostic. Leaves are always simple and entire, most anthers are yellow or orange, and, with the exception of *Lycianthes lycioides*, seeds are discoid with the embryo coiled around the edge of the seed and surrounding the endosperm as is usual in seeds of the Solanoideae. In most species (all those found in Venezuela), inflorescences are fascicles or solitary flowers and lack peduncles; anthers open by small terminal pores, corollas are rotate, and the fruit is an orange or red berry. Seeds are numerous, except in *L. lycioides*. In most characters, plants of *Lycianthes* are much like those of related genera such as *Solanum*, *Physalis*, and *Capsicum*.

Diversity of corolla shape and androecium appearance is shown in Figure 2.

Hair Types

Several hair types, simple, branched, and stellate, are found in the indumentum of Venezuelan species of *Lycianthes*, and these tend to have taxonomic correlation and diagnostic value at the sectional level. In the Venezuelan species, all hairs are uniseriate, and glandular hairs are not found. Simple hairs are usually several cells long with little noticeable differentiation. In section *Simplicipila*, coarse and tawny simple hairs give a strigose appearance. In *Lycianthes acutifolia*, a basal expansion, not unlike that found in many Boraginaceae (pers. obs.), gives the simple hair on the leaf lamina the appearance of arising from a translucent foot. Many species have only simple hairs. Species with branched or stellate hairs often also have simple hairs. Hairs with the radii all arising at one point are termed stellate; when radii arise along the stalk they are referred to as branched (Roe, 1971; Seithe, 1962; Haegi, 1991). On some parts, especially abaxially on the corolla, hairs may be reduced to simpler, difficult-to-interpret types.

Seithe (1962), in her study of hairs in *Solanum*,

examined 25 species of *Lycianthes*. Among these were six that occur in Venezuela: *amatitlanensis, asarifolia, acutifolia (conicibaccata), lenta (varifolia), radiata (goudotii),* and *stenoloba (stephanocalyx).* She concluded that the elaboration of hair types in *Lycianthes* evolved independently from that in *Solanum.* She hypothesized that in *Lycianthes* stellate hairs arose from branched hairs, unlike in *Solanum* where they arose from gland-tipped hairs. Unfortunately, she did not distinguish between the simple, eglandular hairs (*Fingerhaare*) characteristic of many species of *Solanum* and the coarse, tawny strigose hairs of some *Lycianthes,* which seem quite different in nature. These simple hairs in *Lycianthes* may also be independent in origin from those in *Solanum.*

Uses

Fruits of some species, *Lycianthes asarifolia* in Venezuela and elsewhere, are sometimes eaten, and some, *L. moziniana* (Dunal) Bitter and others in Mexico (Williams, 1993; Dean, 1995), even reach fruit markets. *Lycianthes rantonnei* (Carrière) Bitter is grown as an ornamental in upland tropical gardens. No other uses are known.

Chemistry

Lycianthes has a suite of alkaloids comparable to other genera of Solanaceae (Roddick, 1986), but few species have been examined (Bradley et al., 1978; Evans & Somanabandhu, 1980; Lin et al., 1987; Ripperger & Porzel, 1992), none of these species occurring in Venezuela.

Systematics of *Lycianthes*

Lycianthes was divided into a hierarchy of subgenera, sections, and series by Bitter (1920), only some of which are represented in Venezuela. The subgenera and sections in Venezuela are amply distinct and not likely to be confused. Within the sections, however, distinctions are often difficult to make, and species limits are sometimes poorly known. The type species, *Lycianthes lycioides,* has fruits with eight or fewer seeds that are enclosed in sclerenchyma as pyrenes. It constitutes a perhaps monospecific subgenus and section. In the other four sections, seeds are numerous and not enclosed in sclerenchyma. Section *Asaropsis* includes one or perhaps three species of ground creepers. Section *Simplicipila* includes perhaps a dozen species of weak shrubs with strigose hairs. Section *Polymeris* includes many species of night-blooming climbers. Series *Oligochondra* and *Virgatae* are separated by presence or absence of stone cells in the fruit.

Subgenus *Lycianthes* (*L. lycioides*): seeds enclosed as pyrenes.

Section *Lycianthes* (*L. lycioides*): erect, woody shrubs; flowers diurnal; stamens unequal (3+2).

Subgenus *Polymeris* (Dunal) Bitter: seeds numerous, not enclosed in sclerenchyma; fruits sometimes with stone cells.

Section *Asaropsis* Bitter (*L. asarifolia*): plants procumbent; leaves cordiform; flowers solitary, diurnal; stamens equal; stone cells wanting.

Section *Polymeris*: shrubs or climbers; flowers fasciculate, nocturnal; calyx teeth 10 in 2 unequal series; stamens unequal (4+1); stone cells often present.

Series *Oligochondra* Bitter (*L. ferruginea, L. pauciflora, L. stenoloba*): plants high climbing or erect, small shrubs; flowers fasciculate, nocturnal; fruits dangling, stone cells often present.

Series *Virgatae* Bitter (*L. lenta, L. sanctaemarthae*): plants low climbers; flowers fasciculate, nocturnal; fruits dangling, stone cells wanting.

Section *Simplicipila* Bitter (*L. acutifolia, L. amatitlanensis, L. inaequilatera, L. radiata*); subshrubs; flowers fasciculate, diurnal; stamens equal; fruits held erect, stone cells present or not.

Geography of *Lycianthes*

Lycianthes is confined to the Neotropics and to southeast Asia. Most of the species and most of the diversity is in the New World, with distinctive groups in Mexico and Central America. Section *Lycianthes* (*L. lycioides*) is restricted to South American uplands. Section *Asaropsis* includes one (or two) species that grow in lowlands in eastern South America. *Lycianthes asarifolia,* of this section, was recently reported as introduced into Texas (Darwin & Feibelman, 1991). This section may also embrace *L. lysimachioides* (Wall.) Bitter, a wide-ranging southeast Asian species that has similar growth form and anthers, but which has well-developed teeth on the calyx. Section *Polymeris* and its similar series *Oligochondra* and *Virgatae* are widespread at lower and middle elevations in South and Central America and the Antilles. Section *Simplicipila* has a similar range but is not known from the Antilles, and it may not range north of Nicaragua.

Scope of the Present Study

Both authors have studied plants of *Lycianthes* in various countries for more than two decades, but the present focus that led to this paper dates from

funding from binational grants in 1991. This permitted three extensive field trips to cover almost all parts of Venezuela thought to host *Lycianthes* species, also study of a large suite of borrowed herbarium specimens by both authors at the Missouri Botanical Garden, St. Louis. Many other smaller field trips were made in Venezuela during this period, and other herbaria were visited. Many of the species were grown for observation in the St. Louis greenhouse.

Considering the large range sizes of some species and frequent occurrence in disturbed habitats, the number of specimens in herbaria is disappointingly low (D'Arcy, 1973: 632; Nee, 1981). This has meant few observations and scant data in some cases, leading to hesitancy in assigning species names and in documenting ranges outside of Venezuela. Despite our efforts, the genus remains seriously undercollected in Venezuela, and further work should enhance knowledge of the genus.

Lycianthes in Venezuela

In Venezuela we record 11 species of *Lycianthes*. They include procumbent herbs (*L. asarifolia*), erect shrubs (*L. lycioides*), arching subshrubs (*L. amatitlanensis, L. inaequilatera*), and climbers that remain in the understory (*L. lenta*) or climb to the canopy (*L. pauciflora*). All are perennial. Some species have diurnal flowers that generally lack scent, while others have fragrant flowers that are open at night. Night scented flowers have been observed to open just before dusk and to close after dawn. Most species are found at low elevations, but some species (*L. ferruginea, L. radiata, L. acutifolia*) range into cloud forests at upper elevations, and *L. lycioides* is found up to 3500 m elevation. *Lycianthes asarifolia* and *L. lenta* are often adventive in secondary habitats, and the latter, circum-Caribbean in distribution, is often found near the sea.

Taxonomic Treatment

Lycianthes (Dunal) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 180. 1917. Based on *Solanum* sect. *Pachystemonum* subsect. *Lycianthes* Dunal, in DC., Prodr. 13(1): 29. 1852. *Solanum* series *Meiomeris* Dunal, in DC., Prodr. 13(1): 29; 156. 1852. *Solanum* subg. *Lycianthes* (Dunal) Bitter, Bot. Jahrb. Syst. 54: 424. 1917. *Otilix* Raf., Med. fl. 2: 87. 1830. *Solanum* sect. *Lycianthes* (Dunal) Wettst., in A. Engler & K. Prantl, Nat. Pflanzenfam. 4(3b): 22. 1891. TYPE: *Solanum lycioides* L.

Parascopolia Baill., Hist. pl. 9: 338. 1888. TYPE: *Parascopolia acapulcensis* Baill. = *Lycianthes acapulcensis* (Baill.) D'Arcy.

The name *Lycianthes* is conserved against *Otilix* Raf. and *Parascopolia* Baill.

Perennial *herbs, shrubs,* or *vines;* pubescence of simple or branched hairs. *Leaves* often geminate, simple, entire, membranous to coriaceous, petiolate. *Inflorescences* mostly solitary flowers or fasciculate at leaf axils. *Flowers* diurnal or nocturnal, often only a few opening at a time, sometimes showy, mostly 5-merous; calyx cupular, apically truncate, 10-nerved, the nerves often enated into lateral teeth, pubescent or glabrous; corolla white, blue, or purplish, mostly rotate or reflexed, apically subentire or deeply divided; stamens equal or not, anthers yellow (the Venezuelan species), held together in a cone, rarely connate, the pores mostly minute and terminal, rarely elongate, adaxial slits; ovary spherical or conical, style slender, mostly glabrous, stigma capitate, sometimes bilobate; ovules many. *Fruit* a fleshy or juicy berry, mostly red, orange, or yellow, usually globose or nearly so, stone cells (sclerocytes) present in some species; seeds many, mostly discoid, light colored, testa reticulate; embryo coiled around the periphery of the testa.

Key to Species of *Lycianthes* in Venezuela

1a. Leaves either basally cordate or conspicuously oblique, minor leaves often present; corollas white, mostly one opening at a time, diurnal; hairs mostly simple; stamens all alike (*Asaropsis, Simplicipila*).
- 2a. Leaves basally cordate, glabrous; plants creeping or procumbent; flowers solitary, deflexed on erect peduncles held erect above the leaves (*Asaropsis*) ..... *L. asarifolia*
- 2b. Leaves conspicuously oblique, pubescent; plants erect; flowers fasciculate, erect on the pedicels but held beneath the leaves (*Simplicipila*).
  - 3a. Calyx teeth wanting (the 10 nerves slightly elevated and often conspicuous, often splitting in fruit to appear tooth-like) ..... *L. radiata*
  - 3b. Calyx teeth conspicuous, surpassing the margin of the calyx.
    - 4a. Calyx 2 mm long or longer, calyx teeth 2–3 mm long; berry more than 6 mm long.
      - 5a. Corolla more than 9 mm long; fruiting pedicels mostly more than 15 mm long; fruit oblong to conical (often above 1200 m elevation in Venezuela) ..... *L. acutifolia*
      - 5b. Corolla less than 9 mm long; fruiting pedicels less than 15 mm long; fruit globose (not above 1200 m elevation in Venezuela) ..... *L. amatitlanensis*
    - 4b. Calyx less than 2 mm long, calyx teeth less than 0.7 mm long; berry 5–6 mm long ..... *L. inaequilatera*

1b. Leaves basally narrowed or truncate, often symmetrical, minor leaves seldom present; corollas white, blue, or violet, several opening at a time, often crepuscular or nocturnal; hairs mostly branched or stellate; stamens unequal (*Lycianthes, Polymeris*).

6a. Plants erect, branches rigid, sometimes with spinose branches; leaves small (less than 1 cm wide); stamens with 3 longer and 2 shorter filaments; fruit less than 6 mm across; seeds fewer than 8, enclosed in sclerenchyma as pyrenes (*Lycianthes*) *L. lycioides*

6b. Plants generally climbing, branches flexuous, often sprawling, unarmed; leaves large (more than 1.5 cm wide); stamens with 1 longer and 4 shorter filaments; fruits more than 6 mm across; seeds mostly more than 8, the testa entirely visible, not enclosed in sclerenchyma (*Polymeris*).

7a. Calyx lacking teeth ..... *L. sanctaemarthae*

7b. Calyx with conspicuous teeth.

8a. Pubescence of simple hairs; calyx teeth in one series; corolla lobed; fruiting calyx teeth ascending or spreading, almost as long as the fruit ..... *L. stenoloba*

8b. Pubescence of branched or stellate hairs; calyx teeth in two series; corolla subentire or lobed; fruiting calyx teeth reflexed or spreading, much shorter than the fruit.

9a. Leaves evenly puberulent overall with minute stellate hairs, leaf bases mostly truncate or rounded, leaves near the inflorescences mostly less than 4 cm long; fruits less than 9 mm across, lacking stone cells ..... *L. lenta*

9b. Leaves glabrate with scattered coarse stellate hairs, leaf bases mostly obtuse or cuneate, pointed, leaves commonly more than 5 cm long; fruits more than 10 mm across, mostly with stone cells.

10a. Plants copiously pubescent with yellowish or reddish brown hairs, the pedicels tomentose, corolla lobes greenish and the folds white; found between 1200 and 2900 m in Venezuela ..... *L. ferruginea*

10b. Plants glabrescent, pedicels glabrate, corolla mostly uniform yellow; found between 600 and 1500 m in Venezuela ..... *L. pauciflora*

Clave de las Especies de Lycianthes de Venezuela

1a. Hojas basalmente cordadas u oblicuas; hojas menores generalmente presentes; corolas blancas, abriendo una flor por inflorescencia, diurnas; estambres iguales; tricomas generalmente simples (*Asaropsis, Simplicipila*).

2a. Plantas rastreras o procumbentes, glabras, flores solitarias, colgantes sobre pedúnculos erectos y colocadas arriba de las hojas (*Asaropsis*) ..... *L. asarifolia*

2b. Plantas erguidas no enraizando en los nudos, pubescentes, flores fasciculadas, erectas, colocadas debajo de las hojas (*Simplicipila*).

3a. Cáliz sin dientes, los 10 nervios conspícuos y un tanto elevados ..... *L. radiata*

3b. Cáliz con dientes conspícuos exediendo el margen del cáliz.

4a. Dientes del cáliz iguales o mayores de 2 mm de longitud; frutos mayores de 6 mm de longitud.

5a. Corola igual o mayor de 9 mm de longitud; frutos oblongos, cónicos u ovoides; pedicelos fructíferos mayores de 15 mm de longitud; localizada encima de 1500 m de elevación en Venezuela ..... *L. acutifolia*

5b. Corola menor de 9 mm de longitud; frutos globosos; pedicelos fructíferos menores de 15 mm de largo; localizada debajo de 1200 m de elevación en Venezuela ..... *L. amatitlanensis*

4b. Dientes del cáliz menores de 0.7 mm de longitud; frutos 5–6 mm de longitud ..... *L. inaequilatera*

1b. Hojas basalmente truncas o angostas, con frecuencia simétricas; hojas menores rara vez presentes; corolas blancas, azules o violeta, abriendo varias por inflorescencia, con frecuencia crepusculares o nocturnas; estambes desiguales; tricomas generalmente estrellados o ramificados (*Lycianthes, Polymeris*).

6a. Plantas erguidas con ramas espinescentes, tricomas ramificados, hojas pequeñas (menos de 1 cm de ancho); frutos menores de 6 mm de diám., semillas menos de 8, incluídas en pirenos (*Lycianthes*) ..... *L. lycioides*

6b. Plantas generalmente trepadoras o cuando erguidas con ramas apoyantes, inermes, pelos estrellados o simples, hojas grandes (mas de 1.5 cm de ancho); frutos mayores de 6 mm diám., semillas mas que 8, no incluídas en pirenos (*Polymeris*).

7a. Cáliz edentado ..... *L. sanctaemarthae*

7b. Cáliz con dientes subapicales conspícuos.

8a. Plantas con tricomas simples; dientes del cáliz en una serie; corola con el borde lobado; en fruto, los dientes del caliz erguidos y casi tan largos como el fruto ..... *L. stenoloba*

8b. Plantas con tricomas estrelladas o ramificadas; dientes del cáliz en dos series desiguales; corola con el borde casi entero o lobado; en fruto, los dientes del caliz extendidos o reflejos y menores que el fruto.
9a. Plantas en conjunto pubescentes con pelos estrellados diminutos, hojas basalmente truncas o redondas, hojas cercanas de las inflorescencias generalmente menor de 4 cm de largo; fruto menor de 9 mm de ancho, sin células pétrea ..... *L. lenta*
9b. Plantas glabrescentes y con escasos pelos estrellados o tomentosas, hojas basalmente obtusas o cuneadas, hojas generalmente mayores de 5 cm de largo; fruto mayor de 10 mm de ancho, con frecuencia con células pétreas.
10a. Plantas pubescentes, pedicelos tomentosos; corola con los lobos verdes y el pliegue blanco; localizadas en elevacionales entre 1200 y 2900 m ..... *L. ferruginea*
10b. Plantas glabrescentes, pedicelos glabros; corola generalmente con coloración uniforme; localizadas en elevacionales entre 600 y 1500 m ..... *L. pauciflora*

1. Lycianthes acutifolia (Ruiz & Pav.) Bitter, Abh. Naturwiss. Vereine Bremen 24 (1): 453. 1919 [1920]. *Solanum acutifolium* Ruiz & Pav., Fl. peruv. 2: 33, t. 162, fig. b. 1799. TYPE: Peru. Muña, *Ruiz s.n.* (B destroyed, = F photo 2561).

Lycianthes xylopiifolia (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 454. 1919 [1920]. *Solanum xylopiaefolium* Dunal, in DC., Prodr. 13(1): 179. 1852. TYPE: Venezuela. Colonia Tovar, *Moritz 825* (holotype, G-DC, = F photo 6765).

Lycianthes goudotii var. *uberior* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 436. 1919 [1920]. *Lycianthes conicibaccata* Bitter ex Seithe, Bot. Jahrb. Syst. 81: 313. 1962. TYPE: Colombia. Chiquinquita, Boyacá (Bogotá fide Seithe), blühend July 1909, *Frère Félix s.n.* (holotype, M not seen).

Lycianthes xylopiifolia var. *intermedia* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 455. 1919 [1920]. SYNTYPES: Venezuela. Colonia Tovar, *Moritz 345* (BM not seen); *Fendler 974* (G not seen, MO, P).

Lycianthes xylopiifolia var. *maxima* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 455. 1919 [1920]. TYPE: Venezuela. Colonia Tovar, *Gollmer s.n.* (holotype, B not seen).

Lycianthes lehmannii Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 444. 1919 [1920]. TYPE: Colombia. Alto de Cuitambo, Vulkan Sotarâ, *Lehmann* (B not seen, = F photo 2581).

Erect *subshrub* 0.5–2 m high, branches weak, slender, drying brown, sometimes dark or reddish, sparingly ascending-strigose; pubescence of coarse tawny hairs, the bases often expanded and foot-like. *Leaves* unequal-geminate, ovate, mostly narrow, sometimes oblique, 5–7 × 1.5–6 cm, membranous, above sometimes slightly bullate, paler beneath, veins 6–8 on each side, plane or slightly impressed above, elevated beneath, with scattered hairs above, mostly sparingly glabrescent; petioles 3–15 mm long; minor leaves obovate, 1–3 × 1–2 cm, sessile or short-petiolate. *Inflorescences* solitary flowers in leaf axils. Flowers downward-directed; pedicels 1–2.3 cm long, pubescent; *calyx* 2–4 × 3–5 mm, the cup densely strigose, teeth 10 in one series, 2–3(–6) mm long, weak, erect at anthesis, pubescent; corolla white, 8–15 mm × 1–3 cm, lobed ½–⅓ way down, the lobes spreading or recurved, pubescent outside, especially distally; stamens unequal, 4 filaments 1.5–2.5 mm long, 1 filament 2–3 mm long, anthers 2–3 mm long; ovary subglobose to conical, 1–2 × 0.5–1 mm, style 7–7.5 mm long, exserted 2.5 mm, stigma subglobose. *Berry* yellow to orange, conical, ovoid, or oblong, 6–13 × 4–12 mm, stone cells lacking; fruiting calyx 4–5 mm long, applied to the berry, pubescent, the slender teeth erect or spreading, to 5 mm long; fruiting pedicels to 3 cm long; seeds ca. 65 per fruit, yellow, flattened, the testa hardened 2 × 3 mm. Figures 2F, 3, 4.

Dentro de la sección *Simplicipila* esta especie presenta pubescencia áspera, castaño-amarillenta y con los tricomas de base ligeramente expandida, flores solitarias, corolas mayores de 9 mm de longitud; bayas oblongas, cónicas u ovoides, sin células pétreas.

The species has coarse yellowish brown pubescence. Many of the hairs have slightly expanded bases. The mature fruits are conical or ovoid.

Distribution. Venezuela, Colombia, and Peru. Ravine sides and disturbed sites in cloud forests, 800–3300 m elevation. (Map, Fig. 4.) Flowering and fruiting throughout the year.

Representative specimens examined. VENEZUELA. **Distrito Federal**: Alrededor de las Aguaditas, 2 km al norte de la Colonia Tovar, 1970–2000 m, *Steyermark & Delascio 123500* (MO, VEN). **Aragua:** Colonia Tovar, *Benítez et al. 4236* (MY). **Lara:** Parque Nacional Yacambú, *Fernández 3697* (MY). **Mérida:** Monte Zerpa, 1970–2050 m, *Benítez & Otero 4609* (MY). **Miranda:** Silla de Caracas, quebrada Los Palos Grandes, 1700–1800 m, *Morillo & Manara 1600* (MY, VEN). **Táchira:** Selva nublada, río Quinimarí, arriba de Las Copas, 2500–2800 m, *Steyermark et al. 100742* (MY, VEN). **Trujillo:** Selva nub-

Figure 3. *Lycianthes acutifolia*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Fruiting calyx. After *Benítez 4236* (MY).

lada virgen de las montañas de Misisí, carretera Trujillo–Boconó, 2200–2400 m, *Steyermark & Manara 125326* (VEN). **Yaracuy:** Sierra de Aroa, 9 km W de San Felipe, 1100–1500 m, *Liesner & González 10038* (VEN). **Zulia:** Dist. Perijá, on international boundary, headwaters of río Guasare, 2700–3300 m, *Wood & Berry 85* (VEN).

2. Lycianthes amatitlanensis (Coult. & J. D.

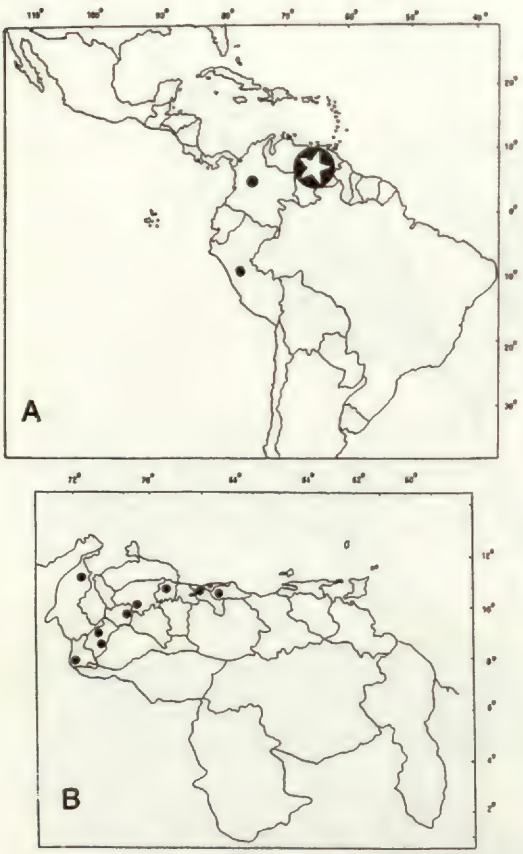

Figure 4. *Lycianthes acutifolia*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Smith) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 441. 1919 [1920]. *Solanum amatitlanense* Coult. & J. D. Smith, Bot. Gaz. (Crawfordsville) 37: 420. 1904. SYNTYPES: Guatemala. Amatitlán, Barranca de Eminencia, *Donnell Smith 1457* (F, = F photo 49339, GH); Alta Verapaz: Cubilquitz, *Tuerckheim 7753* (NY, US), *8488* (C, NY, US).

Lycianthes ulei Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 437. 1919 [1920]. TYPE: Brazil. *Ule 9764* (B not seen, = F photo 2592, NY).

Lycianthes ulei subsp. *dolichodonta* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 438. 1919 [1920]. TYPE: Ecuador. Balao, *Eggers 14409* (A, M not seen, US).

Lycianthes ulei var. *strigulosa* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 438. 1919 [1920]. TYPE: Ecuador. S. Miguel, *Sodiro 114/46* (B not seen).

Subshrub 1–2 mm long, erect or arching and wandlike; stems terete, puberulent; pubescence of coarse, simple, erect, or ascending hairs, often suffused with purple. *Leaves* unequal-geminate, ovate, 14–23 × 4–8.5 cm, apically cuspidate or acuminate, basally narrowed, strongly oblique and slightly decurrent on the petiole, membranous, dark green above, bright green beneath, glabrate on both sides, pubescent along the nerves, more densely so beneath, veins 7–10 on each side, arcuate-ascending, slightly impressed above, slightly elevated beneath; petioles to 0.8–1.5 cm long, mostly strigose; minor leaves subrotund, 1–1.5 × 0.5–0.7 cm with petioles to 5 mm long, sometimes caducous before the major leaves. *Inflorescences* fascicles of 2–5 flowers. *Flowers* diurnal, 1 or 2 open at a time and held below the leaves; pedicels 7–12 mm long, strigose; calyx 1.5–2 × 3–3.5 mm, strigose, with 10 subapical unequal linear teeth in one series, 2.5–3 mm long, strigose, often hidden in the pubescence; corolla white, rotate, 6–9 mm long, lobed halfway down, sparingly pubescent outside; stamens equal, filaments 1.5 mm long, anthers 3–4 mm long, narrowed apically; ovary subglobose or conical, 1–1.5 mm long, style 5–6 mm long, exserted 1.5 mm, stigma capitate. *Berry* globose, red, 6–8 mm across, lacking stone cells; fruiting calyx 6–7 mm long, applied to the berry, teeth erect or spreading, to 5 mm long; fruiting pedicel 13–15 mm long; seeds ca. 100 per fruit, dark brown, 1 × 1.5 mm, the thickened margin less than 0.5 mm wide. Figures 2J, 5.

Especie con pubescencia estrigosa y densa en sus tallos y hojas, los pedicelos florales entre 7 y 12 mm de longitud y los dientes del cáliz de 2.5–3 mm de longitud, bayas globosas sin células pétreas.

This species has conspicuously dense and strigose pubescence on stems and leaves. Its stems are often arching in forest understory. It is similar to *L. inaequilatera*, which has shorter calyx teeth and floral pedicels.

The name "*Solanum amatitlanense*" appeared as a nomen nudem in Enum. Pl. Guatemala (4: 110. 1895).

Distribution. Venezuela, Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Bolivia. Wooded slopes and along ravines of cloud forests, 500–1200 m elevation. (Map, Fig. 6.) Flowering and fruiting through the year.

Pollination of this species was studied in Panama by de Nevers (1986), who reported vibratile pollen extraction by two species of halictid bees. The flowers have no odor and no nectar and are visited mainly in the morning when they are illuminated by sunlight.

Representative specimens examined. VENEZUELA. **Sucre:** Camino a Mundo Nuevo-Manacal, 18–20 km NW of Irapa, 500–700 m, *Morillo 2519* (VEN); Peninsula de Paria, *Knapp & Mallet 6766* (BH, MY), *Steyermark & Liesner 120772* (MO, NY, VEN), *Steyermark & Rabe 96125* (P, VEN), *Steyermark et al. 121528* (VEN), *121593* (VEN). **Yaracuy:** Sierra de Aroa, río Carabobo, 800–1200 m, *Liesner & González 9773* (VEN).

Figure 5. *Lycianthes amatitlanensis*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower. After *Steyermark 121528* (VEN).

3. Lycianthes asarifolia (Kunth & Bouché) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 423. 1919 [1920]. *Solanum asarifolium* Kunth & Bouché, Index Sem. Hort. Berol. p. 10. 1845. *Solanum violifolium* var. *asarifolium* (Kunth & Bouché) Hassl., Repert. Spec. Nov. Regni Veg. 15: 221. 1918. TYPE: cultivated in Berlin from seed from Caracas (holotype, B destroyed, = F photo 2562).

Solanum violaefolium var. *majus* Dunal, in DC., Prodr. 13(1): 164. 1852. TYPE: Bolivia. Santa Cruz, *d'Orbigny 619* not seen.

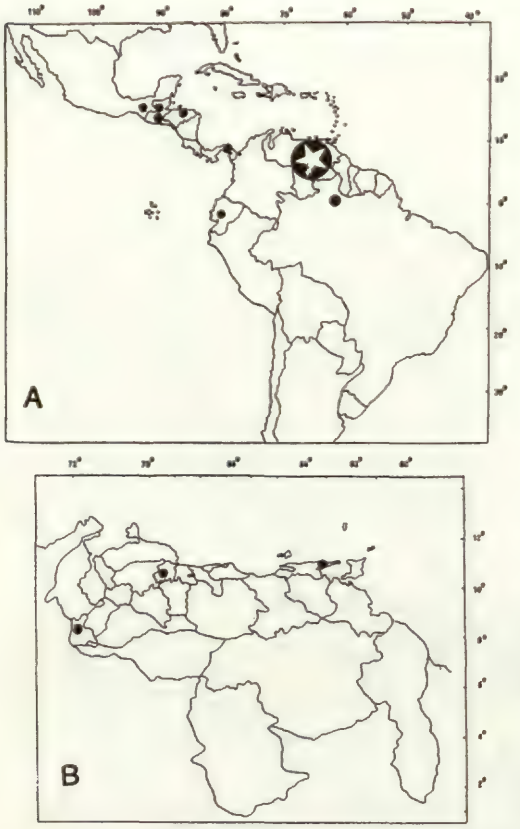

Figure 6. *Lycianthes amatitlanensis.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Solanum chodatianum Huber, Bol. Mus. Paraense Hist. Nat. 4(4): 602. 1906. TYPE: Brazil. Villa de Contamana, 15 Dec. 1898, *Huber 1336* (holotype, MG not seen, = F photo 45292).

Solanum violaefolium fo. *lilaciniflora* Hassl., Trab. Mus. Farm. Fac. Cienc. Med. Buenos Aires 21: 106. 1909. TYPE: Paraguay. Pilcomayo, *Rojas 605* not seen. [Synonymy taken from Barboza & Hunziker (1992: 31).]

Solanum violifolium var. *majus* fo. *chacoense* Hassl., Repert. Spec. Nov. Regni Veg. 15: 220. 1918. TYPE: Paraguay. Lower Pilcomayo, *Rojas 275* (MO).

Solanum violifolium var. *asarifolium* fo. *decadontum* Hassl., Repert. Spec. Nov. Regni Veg. 15: 221. 1918. SYNTYPES: Paraguay. Pilcomayo River, *Morong 920* (G not seen, MO); *Rojas 605* not seen.

Creeping *herb,* stems slender, sparingly pubescent, rooting at the nodes, stoloniferous; pubescence of weak, collapsing, mostly erect, simple hairs. *Leaves* solitary, ovate, 3–10 × 4–10(–15) cm, apically rounded or obtuse, basally deeply cordate, dark green and sometimes shiny above, matte and lighter beneath, membranous, glabrous, veins 3–4 on each side, strongly ascending, sparingly branched; petioles with purplish tones, 3–14 cm long, canaliculate, sometimes with scattered simple hairs. *Inflorescences* solitary, the flowers held above the leaves. *Flowers* diurnal, inodorous, reflexed on the pedicels; pedicels often white or purplish, 4–9 cm long, 0.5–1 mm thick; calyx pale, 3–5 × 3–4 mm, angled, the margin undulate-denticulate, glabrate inside and out, sometimes with sparse hairs on the costas, lateral teeth absent but the 10 nerves evident on drying; corolla white or pale-yellowish, outspread or reflexed, 0.6–1.1 × 1.2–2.2 cm, the margin almost entire; stamens equal, filaments 1–3 mm long, glabrous, anthers held together in a cone, 2.5–3 mm long, the pores extending slightly toward the sides of the anther; ovary conical or subglobose, 1.5–2 mm across, style 5–6 mm long, exserted 1 mm, stigma hardly expanded, subglobose. *Berry* orange-red, compressed-globose, 8–25 mm × 0.7–2 cm, lacking stone cells; fruiting calyx 5–9 × 11–17 mm, not splitting at the sinuses; seeds ca. 70 per fruit, grayish brown, 2 × 2.5 mm long, the margin thickened. Figures 2E, 7; Saunders, Refug. Bot. 4, t. 255. 1871, as *Solanum asarifolium*; Martius, Fl. Brazil 10, t. 4, 12. 1846 (calyx and stamens), as *Solanum asarifolium*; Benítez de Rojas, 1974: fig. 12; Steyermark & Huber, 1978, t. 288; Huber, 1906: 603, fig. 7 (flower), as *Solanum chodatianum.*

Unica especie de hábito prostrado y estolonifero de todas las conicidas de *Lycianthes* en Venezuela, presenta sus hojas conspicuamente cordiformes, las flores solitarias colgantes sobre pedúnculos erectos y los cálices edentados, bayas comprimido-globosas sin células pétreas.

Common names and uses. "Ajicillo," "Barba de Tigre," "Childa," "Huevo de Sapo," "Nicua." Fruits are eaten out of hand and also made into jams.

This is the only species with a prostrate habit among Venezuelan species of *Lycianthes,* presenting its conspicuously cordiform leaves on erect petioles and solitary flowers deflected on erect peduncles. The calyces usually lack noticeable teeth.

Distribution. Venezuela, Bolivia, Peru, Paraguay, southern Brazil, and northeastern Argentina. Deciduous and semi-deciduous woods near moist places, 50–1000 m. Also a component of adventive and weedy vegetation in croplands. (Map, Fig. 8.) Flowering and fruiting throughout the year.

This species is similar to *Lycianthes repens* (Spreng.) Bitter of southeastern Brazil, which is said to differ (Bitter, 1920: 426) in having smaller leaves, shorter stalks, and distinctive hairs. We have seen only two collections that were cited by Bitter under this name. One of these, *Dusén 11315* (F, MO) from Paraná, Ponta Grossa, has two unequal but well-developed leaves at each node. The

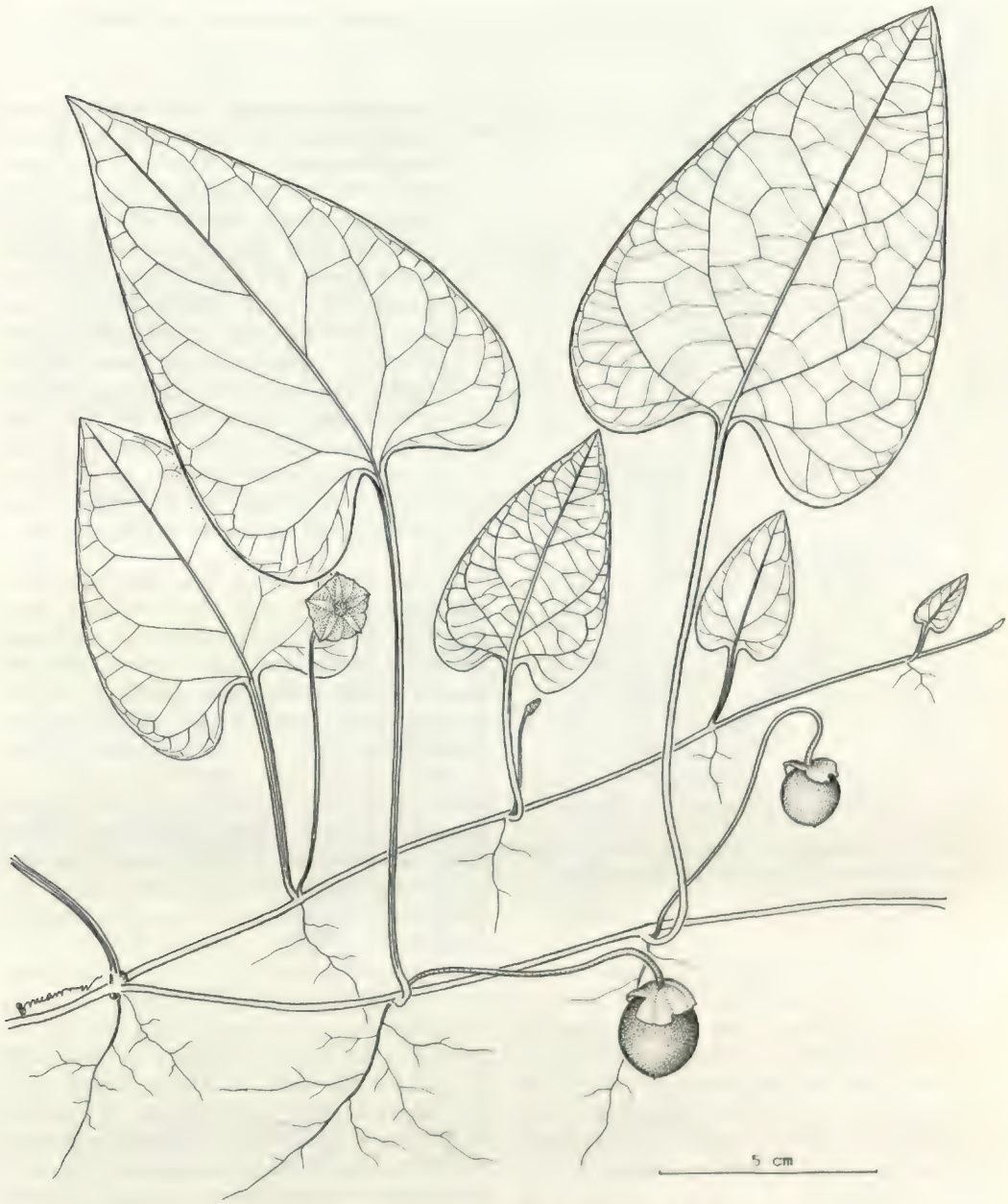

Figure 7. *Lycianthes asarifolia*. Flowering and fruiting stems. After *Licata et al. 32* (MY).

other specimen, *Pohl 5407* (F), without locality, has solitary major leaves and sessile minor leaves like many plants from elsewhere. The Dusén specimen is the only one we have seen with well-developed, long-petiolate minor leaves. The original description of the basionym, *Boldoa repens* Spreng. (Syst. Veg. 1: 179. 1825) and Bitter's description also note unequally paired leaves. While the *Dusén* collection does have small leaves and peduncles, except for the well-developed minor leaves it seems to be conspecific with plants we have identified as *L. asarifolia*. If *L. asarifolia* and *L. repens* are actually the same, then *L. repens* is the prior and correct name. We continue use of *L. asarifolia* for this species, a name that has been used in many publications, rather than substituting the unfamiliar and uncertainly equivalent name *L. repens*. Bitter cited a specimen, "*Otto* ex hb. Kurt Sprengel," which

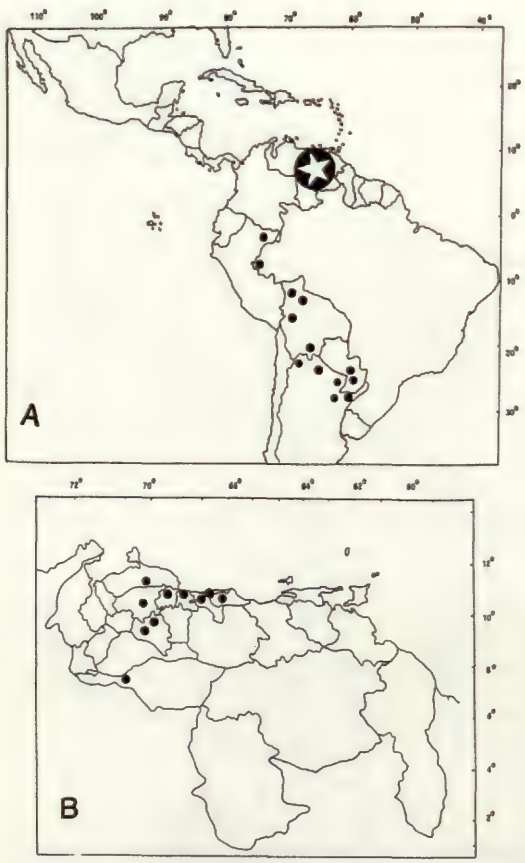

Figure 8. *Lycianthes asarifolia.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

would have served as a type. If *L. repens* is recognized as the correct name, then *Solanum violaefolium* Schott (in Sprengel, Syst. Veg. 4 (appendix): 403. 1827) may also be a synonym. Bitter placed *Solanum violaefolium* into synonymy under *L. repens*, but Schott's description notes that the calyx is "*10fidis*," seemingly contrary to the truncate, nearly edentate calyces found in our species.

Representative specimens examined. VENEZUELA. **Distrito Federal:** S Naiguatá, vertiente N de la Cordillera de la Costa, 600–800 m, *Morillo & Manara 2022* (VEN). **Apure:** Boca del Uribante, *Trujillo & Fernández 10597* (MY). **Aragua:** Río Hondo, km 32 carretera hacia Choroní, 800 m, *Benítez & Rojas 3993* (MY). **Carabobo:** La Toma de Valle Seco, Dist. Puerto Cabello, 100–200 m, *Benítez & Pons 4651* (MY). **Cojedes:** Las Tucuraguas, Mpio. Angel Bravo, 700 m, *Delascio & López 12838* (VEN). **Falcón:** Parque Nacional Quebrada de la Cueva El Toro, 600–900 m, *Liesner et al. 7803* (MY, VEN). **Lara:** Barquisimeto, *Saer 263* (VEN). **Miranda:** near río Guaire between Los Palos Grandes and Dos Caminos, 940 m, *Steyermark 60971* (MY, VEN). **Portuguesa:** Carretera Mesa Cavacas-Biscucuy, *Stergios & Aymard 4451* (MY, PORT). **Yaracuy:** Finca Antonia, San Felipe, 250 m, *Ferrari 790* (MY).

4. **Lycianthes ferruginea** Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 339. 1919 [1920]. *Solanum ornatum* Morton, Contr. U.S. Nat. Herb. 29(1): 59. 1944. SYNTYPES: Venezuela. Aragua: Colonia Tovar, *Moritz 1642* (B destroyed, = F photo 2572, BM not seen, = MY photo; HBG not seen, MO, US); Colonia Tovar, *Golmer s.n.* (B not seen); *Fendler 991* (BR, G not seen, GOET not seen, NY–2). [Although we have seen duplicates of specimens cited by Bitter in the original protologue, we only saw one specimen that he actually cited. This specimen accords with our concept of the taxon and with all the duplicates noted, but we chose not to designate a lectotype without opportunity to review the material again.]

Much-branched *shrub* or *vine*, often high-climbing, branches often at right angles or zigzag, young growth densely ferrugineous pubescent, stems glabrescent; pubescence of reddish or yellowish sessile and stalked stellate hairs, mostly with 3–5 radii, and simple hairs. *Leaves* solitary, ovate or narrowly ovate, 3.4–12 × 2–6 cm, basally obtuse or rounded, sometimes slightly decurrent on the petiole, apex acute, membranous, densely stellate-pubescent on both sides, glabrescent and dark above, brownish yellow beneath, veins 3–4 on each side, mostly slightly impressed above, elevated and conspicuous beneath, minor reticulate venation mostly evident beneath; petioles 0.4–1.7 cm long. *Inflorescences* fascicles of 2–4(–5) flowers, mostly near the branch tips. *Flowers* diurnal, one or two opening at a time; pedicels 0.8–1.7 cm long, tomentose; calyx 3–7 × 3–8 mm, tomentose, teeth 10 in 2 unequal series, erect or spreading, 0.5–4 mm long, sometimes appearing only as costas on the calyx cup; corolla white, sometimes greenish on the lobes, rotate, 0.9–1.5 cm long, 1.8–3 cm wide, entire or subentire, the lobes conspicuously thicker, glabrous outside overall, the lobes sometimes minutely ciliolate with reduced curved hairs, sometimes with small tufts of stellate hairs on the lobe tips, glabrous within; stamens unequal, 4 filaments 1–2 mm long, the fifth 2–4.5 mm long, anthers 2.5–3 mm long; ovary ovoid, 2–4 × 1–3 mm, glabrous, style 6–7 mm long, glabrous, exserted 1 mm, stigma subclavate. *Berry* orange-red, subglobose, 10–20 mm across, with 2–4 stone cells; fruiting calyx slightly accrescent, the cup 4–6 mm long, applied to the berry, sometimes splitting irregularly, the teeth slightly reflexed, not accrescent; seeds ca. 36

Figure 9. *Lycianthes ferruginea*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Fruiting calyx. After *Benítez 5148* (MY).

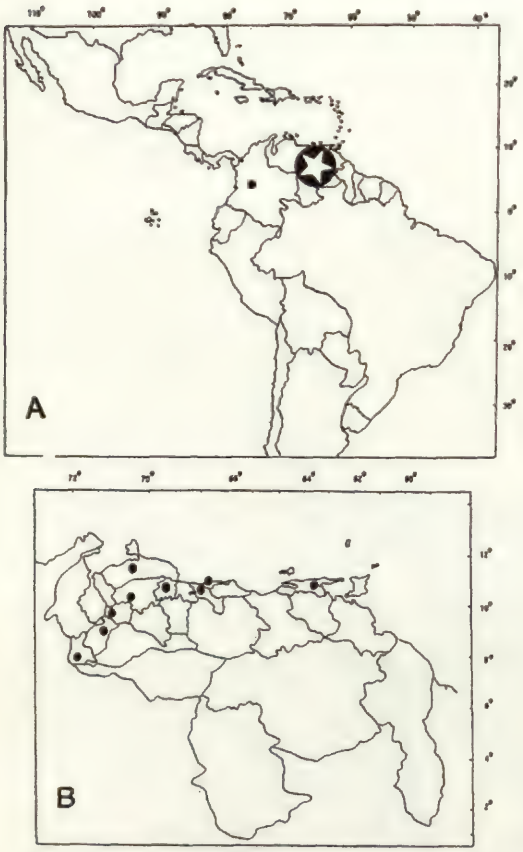

Figure 10. *Lycianthes ferruginea*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

per fruit, yellowish brown, 3–3.5 × 3.5–4 mm, the thickened margin ca. 0.7 mm wide. Figures 2A, 9.

En esta especie el cáliz presenta 10 dientes en dos series; la corola generalmente muestra los lobos conspicuamente verdosos y engrosados y el pliegue blanco; las bayas son subglobosas, sin células pétreas o desde 1 hasta 4 por fruto.

This species is much like *Lycianthes pauciflora*, differing in its conspicuously dense pubescence and corolla color. The calyx lobes of the flowers of this species vary greatly in length and appearance, sometimes appearing as short points spreading from the calyx apex and other times as slender tomentose teeth arising from low on the sides of the calyx. A difference between this species and *L. pauciflora* that was not noted in the key to species is in the coloration of the corollas when seen from outside; in *L. ferruginea* the lobes are green and the folds white, while in *L. pauciflora*, the entire surface is white.

This species is also similar to *L. armentalis* J. L. Gentry from Central America, but that species has pubescent corollas, and so far as is known, equal stamens. It also resembles *L. jelskii* (Zahlbr.) Bitter from Peru, but we cannot judge well from the photo of the type of that species.

Distribution. Colombia. Cloud forests, 1200–2900 m elevation. (Map, Fig. 10.) Flowering and fruiting throughout the year but most flowering from April to August.

Representative specimens examined. VENEZUELA. **Distrito Federal:** El Junquito to Colonia Tovar, 1770 m, *Davidse 4035* (VEN). **Aragua:** Colonia Tovar to El Aguacatal, *Benítez et al.* 4235 (MY). **Falcón:** Sierra de San Luis, 1500 m, *Demey* (MY-86695, CORO). **Lara:** between Cubiro & La Escalera, 1600–2000 m, *Steyermark et al. 110242* (MY, VEN). **Mérida:** Caserío El Portachuelo, NW of Guaraque, 2000 m, *Marcano-Berti & López-Palacios 1758* (MER, MY). **Miranda:** Cortada del Guayabo, *Tamayo 397* (VEN). **Táchira:** above Betania, below Páramo de Tamá, 2530 m, *Steyermark 57433* (MY, VEN). **Trujillo:** El Paramito, near Escuque, *Lasser 1203* (VEN). **Yaracuy:** Los Quinquines, road to La Candelaria, *Diederichs 173* (VEN).

5. Lycianthes inaequilatera (Rusby) Bitter, Abh. Naturwiss. Vereine Bremen 24 (1): 439. 1919 [1920]. *Bassovia inaequilatera* Rusby, Mem. Torrey Bot. Club 6: 90. 1896. *Brachistus inaequilaterus* (Rusby) Rusby, Bull. New York Bot. Gard. 4: 470. 1907. SYNTYPES: Bolivia. Between Tipuani and Guanai, *Bang 1708* (B not seen, G, M not seen, MO).

Erect or wandlike *subshrub* 1–2 m tall, branches flexuous, arching, strigose, adult branches somewhat glabrescent, ridged, often drying dark brown; pubescence of coarse simple hairs. *Leaves* unequal-geminate, narrowly ovate, 16.5–20 × 4–6.5 cm, apically acuminate, sometimes abruptly so, basally strongly oblique, one side obtuse or rounded, the other decurrent on the petiole, membranous, lighter beneath, glabrate or with scattered hairs on both sides, especially along the nerves, more so beneath, ciliate, veins 6–8 on each side, major veins plane or slightly impressed above, slightly elevated beneath; petioles 0.5–0.8 cm long, compressed; minor leaves ovate, 2.3–3.6 × 1.3–1.6 cm, subsessile. *Inflorescences* fascicles of (1–)4 flowers. *Flowers* with pedicels 2–3 cm long, strigose; calyx 2.5 × 2 mm, pilose, teeth 10, slightly unequal in one series, subulate, 0.5–0.7 mm long, strigose; corolla white, rotate, 8–9 × 9–10 mm, lobed ½–⅓ way down, pilose outside; stamens equal, filaments 3.5 mm long, anthers 2.5–3 mm long; ovary ovoid, 1 × 0.5–0.6 mm, style 6.5 mm long, exserted 2 mm, stigma capitate. *Berry* red, subglobose, 5–6 mm across, without stone cells; fruiting calyx accrescent, the cup 3–4.5 mm long, the teeth slightly ac-

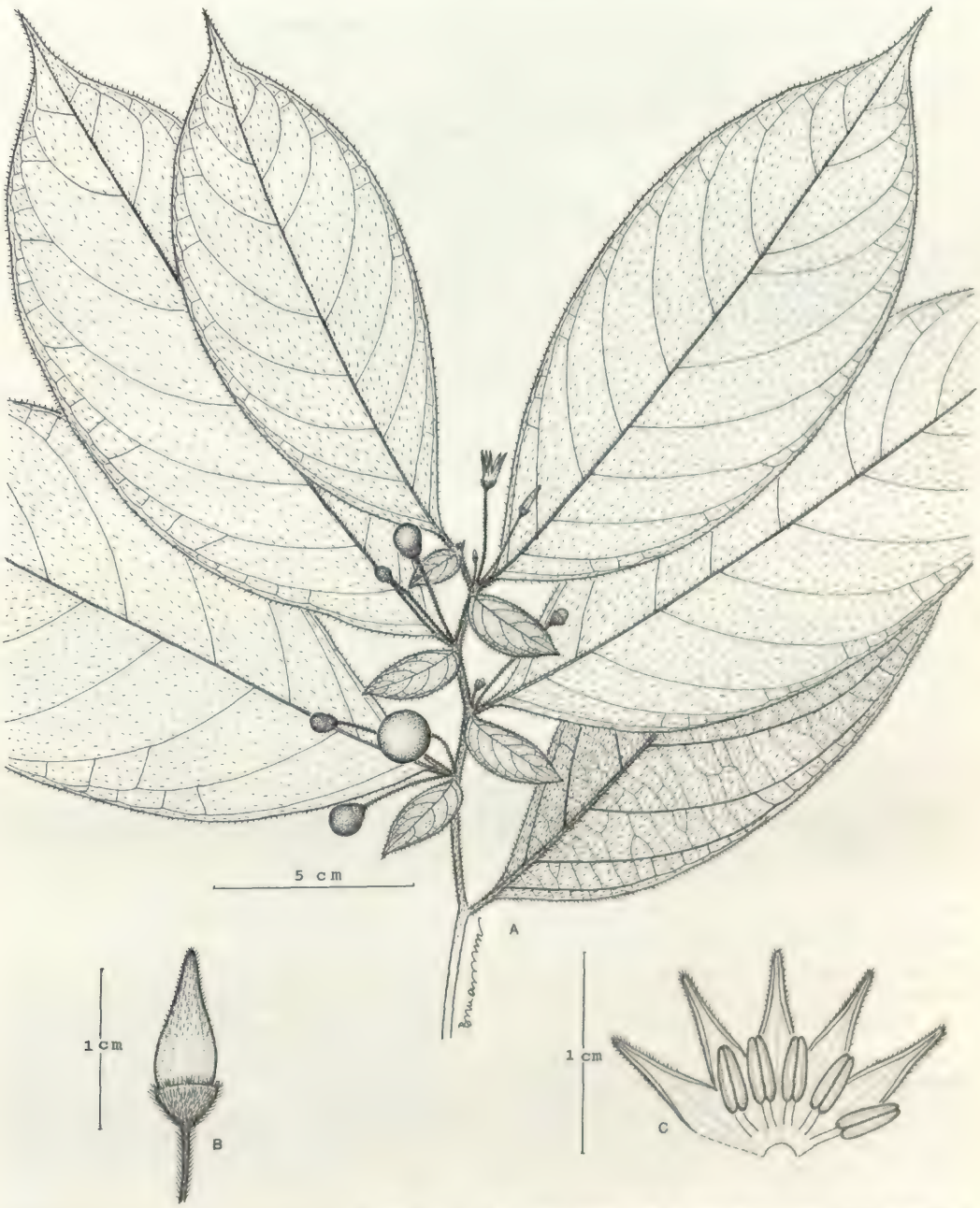

Figure 11. *Lycianthes inaequilatera*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower. A. After *Stergios et al. 6360* (MY); B, C. After *Davidse 18899* (VEN).

crescent, fruiting pedicels 2 mm long; seeds ca. 70 per fruit, yellowish brown, 1.5–1 mm across, the conspicuously thickened margin 0.5 mm wide. Figures 2I, 11.

Se caracteriza por ser pubescente, con hojas menores conspícuas, los dientes del cáliz en número de 10, ligeramente desiguales, en una serie y subulados, los cuales son generalmente poco conspícuos en fruto, bayas subglobosas, sin células pétreas.

This species closely resembles *L. amatitlanensis*, from which it differs in its lesser pubescence and shorter calyx teeth, which are usually less conspicuous in fruit, and longer pedicels.

Distribution. Venezuela and Bolivia. Cloud for-

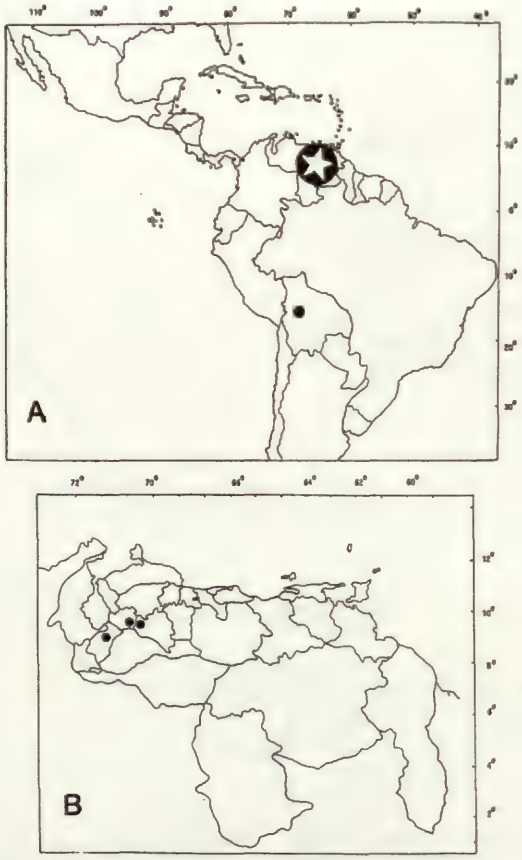

Figure 12. *Lycianthes inaequilatera.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

ests and along ravines, 1500–1900 m elevation. (Map, Fig. 12.) The six collections seen from Venezuela are all in fruit, made scattered throughout the year. Further collecting should reveal the presence of this species in other countries.

Representative specimens examined. VENEZUELA. **Mérida:** Dist. Andrés Bello, between quebrada El Trigal and quebrada Zerpa, 10–14 km SE of La Azulita, 1600–1900 m, *Davidse & González 18899* (NY, VEN). **Trujillo:** 13 km E of Boconó, 1 km W of Guaramacal, 1600 m, *Liesner et al. 12833* (MY, VEN). **Portuguesa:** Dist. Sucre, Los Paramitos, SE of Biscucuy, 1000–1500 m, *Stergios et al. 6360* (MY, PORT).

6. Lycianthes lenta (Cav.) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 364. 1919. *Solanum lentum* Cav., Icon. 4: 4, plate 308. 1797. *Solanum virgatum* Lam. var. *lentum* (Cav.) O. E. Schulz, in Urban, Symb. Antill. 6: 189. 1909. TYPE: cultivated Madrid, seed from Mexico (holotype, MA).

Solanum cumanense Roem. & Schultes, Syst. Veg. 4: 662. 1819. TYPE: Venezuela. Cumaná, *Humboldt 71* (holotype, P, = IDC microfiche 4316, = F photo, 002896).

Solanum lentum var. *echinatum* Dunal, in DC., Prodr. 13(1): 173. 1852. TYPE: Mexico. Without collector (G not seen, = F photo 34120). [The typification of this species was interpreted by Nee (1986: 97) to be based on specimens of Sesse & Mocino now at F, MA, and G, including the one of which we have seen a photo.]

Solanum sylvaticum sensu Schlecht., Linnaea 5: 112. 1830, non Dunal (1852), fide Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 364. 1919 [1920]. Based on material from Veracruz, Mexico.

?*Solanum quadriflorum* M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles 12(1): 139. 1845. TYPE: Mexico. *Galeotti 1231* (holotype, BR not seen; isotype, P not seen, = F photo 39198).

Solanum declinatum Sessé & Moç., Fl. Mex. ed 2: 54. 1893 [1894]. SYNTYPES: Mexico. Teuzitlan specimen not indicated. [Nee (1986: 97) cited as authentic material: *Sessé & Mociño 1525* (F, MA not seen, = F photo 48223) and *Sessé & Mociño 5366* (F, MA not seen, = photo 48235).]

Solanum lambii Fernald, Bot. Gaz. (Crawfordsville) 20: 536. 1895. TYPE: Mexico. Sinaloa: Villa Union, *Lamb 446* (holotype, GH not seen; isotype, MO).

Solanum nocturnum Fernald, Proc. Amer. Acad. Arts 35:

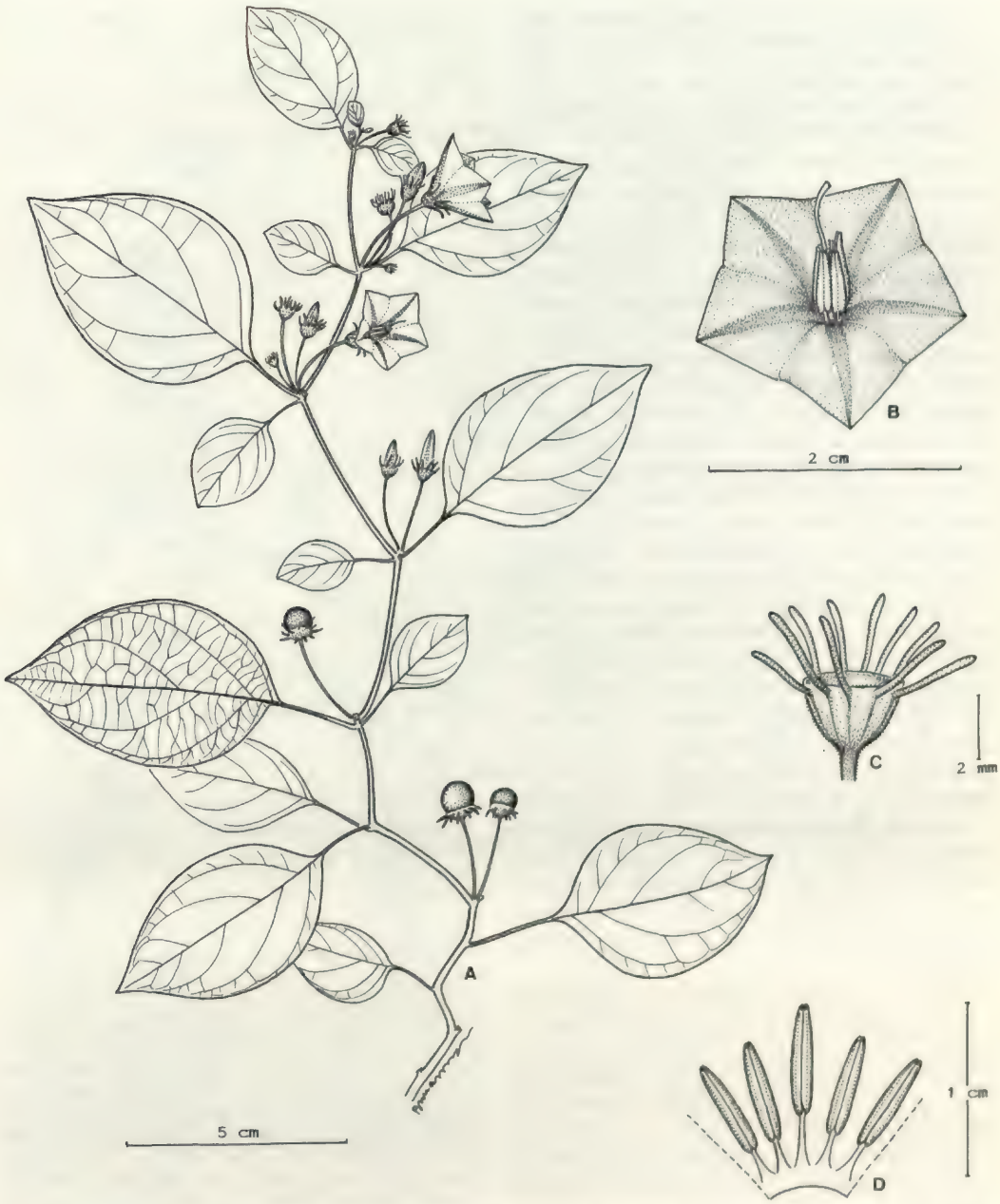

Figure 13. *Lycianthes lenta*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Flower bud.—D. Stamens inserted on corolla. After *Bunting 4433* (MY).

570: 1900. SYNTYPES: Mexico. Oaxaca: *Palmer 533* (GH not seen); Tehuantepec, *Seler 1625* (GH not seen).

Lycianthes lenta var. *endopsila* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 367. 1919 [1920]. SYNTYPES: Venezuela. Caracas, *Humboldt 748* (B not seen); *Vargas s.n.* (lectotype, designated here, US-601441).

Solanum virgatum Lam. var. *caracasanum* O. E. Schulz, in Urban, Symb. Antill. 6: 190. 1909. TYPE: Venezuela. Near Cura, *Humboldt 748* (holotype, P).

Lycianthes lenta var. *scotinophila* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 367. 1919 [1920]. TYPE: Venezuela. Valle del Aragua bei San Mateo, *Otto 788* (holotype, B destroyed).

Lycianthes pauciflora (Vahl) Bitter subsp. *tobagoensis* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 343.

1919 [1920]. SYNTYPES: Tobago. *Broadway 4523* (holotype, B destroyed); Trinidad, *Crueger 148* (GOET not seen).

Lycianthes variifolia Standl., Field Mus. Bot. 4: 259. 1929. TYPE: Belize. Tower Hill, *Karling 13* (holotype, F). [Taken from synonymy of Gentry & Standley (1974).]

Shrub to 3 m, erect, climbing or sprawling, stems slender, drying greenish, young branches pubescent; pubescence of stalked, stellate hairs with 4–6 rays. *Leaves* solitary or geminate, ovate, sometimes narrowly or broadly so, 4.4–10 × 2.6–5 cm, apically rounded, obtuse, or short-acuminate, basally rounded, truncate or slightly cordate, sometimes short-decurrent on the petiole, membranous, softly pubescent, veins 3–4 on each side, slightly elevated; petioles 1–2 cm long. *Inflorescences* fascicles of 5 or fewer flowers, sometimes leaving a cicatrix from fallen pedicels. *Flowers* nocturnal, strongly sweet-scented, only a few open at a time; pedicels 1–2.5 cm long, slender, pubescent; calyx 3–4 × 3–5 mm, sparingly pubescent, with 10 subapical teeth in two unequal series, 1–2(–3) mm long, erect or spreading; corolla white or bluish, 1.5–3 × 3–5 cm, lobed less than ⅓ way down, the lobes conspicuously thicker, puberulent in bud with stellate and reduced hairs, glabrescent except at the tips; stamens unequal, 4 filaments 1.5–2 mm long and anthers 3–4 mm long, the fifth filament 3.5–8 mm long and anther 5–6 mm long; ovary ovoid, 1–1.5 × 1 mm, glabrous, style 8–12 mm long, exserted 2 mm, stigma subemarginate or clavate. *Berry* red or orange-red, subglobose, 6–9 mm across, stone cells lacking; fruiting calyx 6–8 mm long, generally applied to the berry, teeth spreading, hardly accrescent; seeds ca. 35 per fruit, pale yellow, 2 × 2.5 mm, the thickened margin ca. 0.5 mm wide. Figures 1C, 2C, 13; Nee, 1986: p. 101. fig. 10.

The name *Solanum nocturnum* is placed into synonymy here based on Fernald's description.

Es de amplia distribución en áreas de alturas bajas y se caracteriza por sus tallos castaño-claros y ramificación densa, los dientes del cáliz en dos series desiguales y los frutos carecen de células pétreas.

The species may be recognized by its bright brown stems, dense branching, and large corolla diameters.

Distribution. Mainly Caribbean in distribution: Mexico, Belize, Guatemala, El Salvador, Nicaragua, Trinidad and Tobago, Cuba; Venezuela. Deciduous woods and thickets, sea level to 500 m. Often near the sea, but actually of wide distribution in medium and low elevations. (Map, Fig. 14.) The species flowers and fruits throughout the year.

Representative specimens examined. VENEZUELA. **Apure:** Parque Nacional Santos Luzardo, isla El Vapor, 40 m, *Duno et al. 184* (MY). **Aragua:** Ocumare de La Costa, 0–400 m, *Badillo 1816* (MY); Carretera Cagua–La Villa de Cura, 4 km al S de Cagua, *Bunting 4433* (MY). **Barinas:** Río Caparo, E del Cantón, 100 m, *Steyermark 102180* (MO, NY, VEN). **Carabobo:** Quebrada María Teresa, Dist. Valencia, 500 m, *Benítez & Rojas 3214* (MY). **Cojedes:** Entrada a El Baúl, *Trujillo et al. 16662* (MY). **Falcón:** Dist. Silva, NE of La Soledad, 5 m, *Steyermark & Manara 110995* (MO, NY, VEN). **Lara:** Santa Rosa, *Pittier 13088* (MO, NY, VEN). **Miranda:** Paparo, río Chico, 10 m, *Aristeguieta 3994* (MO, VEN). **Nueva Esparta:** Cerro Los Cedros, SW of San Francisco, Península de Macanao, 100–300 m, *Benítez 2614* (MY). **Sucre:** Parque Nacional Mochima, El Tacal, *Cumana 1850* (IRBR, MY). **Yaracuy:** Finca Los Apamates, La Llanada, between Urama & San Felipe, *Romero 486* (MY). **Zulia:** Carretera Caja Seca–Bobures, *Bunting 5808* (MO, VEN, VZU).

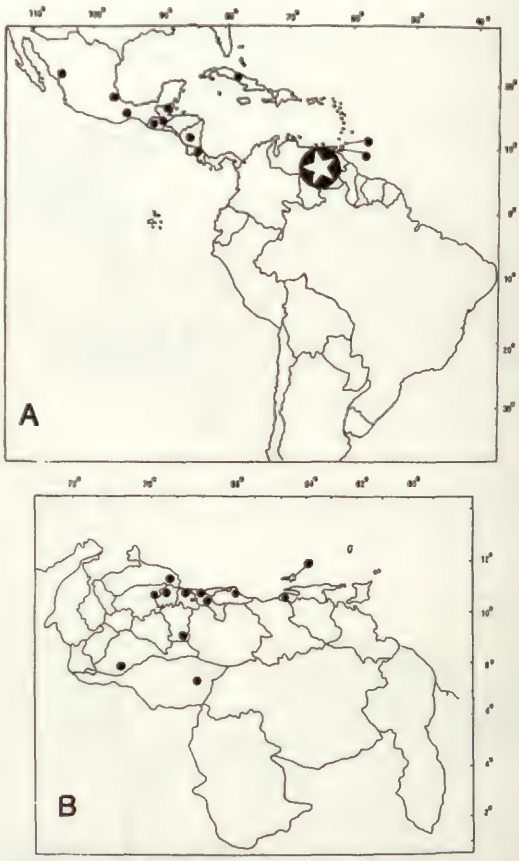

Figure 14. *Lycianthes lenta.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

7. Lycianthes lycioides (L.) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 181. 1917. *Solanum lycioides* L., Syst. Nat. ed. 12, 2: 174. 1767; Mantissa Pl. 1: 46. 1767. TYPE: Peru. LINN 248.48 (lectotype, designated by Knapp & Jarvis (1990)).

Solanum lycioides var. *tomentosa* Dunal, Hist. Nat. *Solanum* 174. 1813. *Solanum candicans* Dunal, Sol. Syn.

Figure 15. *Lycianthes lycioides*.—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower.—D. Pyrenes (seeds enclosed in sclerenchyma). After *Benítez 5373* (MY).

23. 1816. *Lycianthes candicans* (Dunal) Hassl., Annuaire Conserv. Jard. Bot. Genève 20: 181. 1917. *Lycianthes lycioides* subsp. *tomentosa* (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 327. 1919 [1920]. Based on *Solanum lycioides* Ruiz & Pav., Fl. peruv. 2: 41, 5. 177b, non L. TYPE: Peru. Huanuci & Tarmae (G not seen, = F photo 34114, MPU not seen).

Solanum phillyreoides Dunal, Sol. Syn. 24. 1816. TYPE: Colombia. Fluvium Magdalenae, (holotype, P, = IDC microfiche 4375).

Solanum pseudolycioides Rusby, Bull. Torrey Bot. Club 26: 193. 1899. SYNTYPES: Bolivia. La Paz, 10,000 ft., *Rusby 833*; 12,000 ft, *Rusby 835* (both NY neither seen); *Bang 32* (NY not seen).

Solanum lyciiforme Dammer, Engl. Jahrb. 37: 168. 1905.

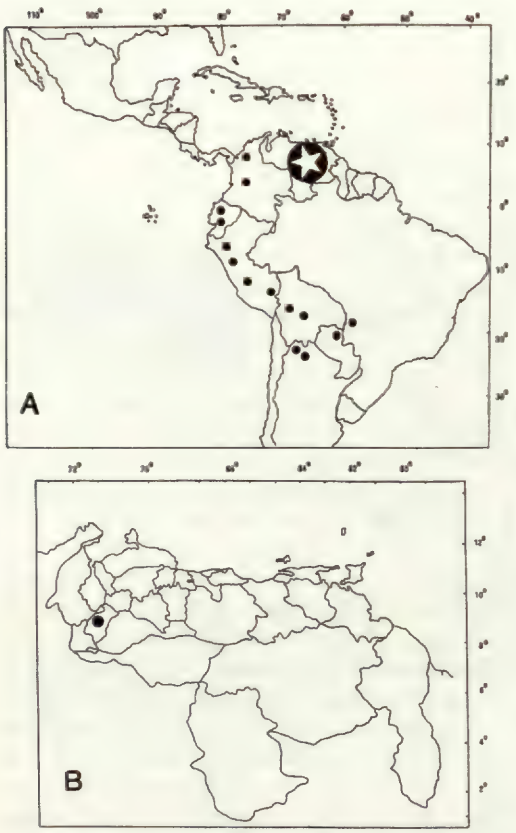

Figure 16. *Lycianthes lycioides.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

SYNTYPES: Argentina. Jujuy: Santa Catalina, *Claren 11550*; Yavi, *Fries 985* (B not seen, CORD not seen). [Synonymy of Bitter, 1919 [1920]; Morton et al., 1976: 33; Barboza & Hunziker, 1992.]

Erect *shrubs* 0.5–1 m tall, much branched, young branches green, tomentose, adult branches strongly lignified, grayish, glabrescent, conspicuously lined, the shoots sometimes becoming spinose; pubescence of erect, sparingly branched hairs. *Leaves* solitary, often with short internodes and appearing dense or even fasciculate, elliptical, smaller leaves sometimes obovate, 0.6–2.5 × 0.3–1.1 cm, membranous or papery, both sides densely fine-pubescent, glabrescent, remaining apically tufted, veins 3–5 on each side, slightly elevated; petioles 2–4 mm long. *Inflorescences* fascicles of 3 or fewer flowers. *Flowers* diurnal, showy; pedicels 0.5–1.6 cm long; calyx 2–3 × 0.3–0.5 mm, pubescent to glabrate, teeth 10 in 2 unequal series, the upper series 1 mm long, the lower teeth 0.5 mm long, erect; corolla blue-violet with a yellow eye, rotate, the margin almost entire, the lobes strongly contrasting, 1 × 2–2.5 cm, mostly glabrate; stamens unequal, 3 filaments 1.5–2.5 mm long, 2 filaments smaller, 0.5–1.2 mm long; anthers yellow to orange, 1.8–2.7 mm long; ovary ovoid, 1–2 × 1–1.2 mm, style 4–5 mm long, exserted 1 mm and curved, stigma bilobate. *Berry* orange, depressed-globose, 2–6 mm across, with 7–8 stone cells (pyrenes); fruiting calyx hardly accrescent, applied to the berry, the teeth spreading; fruiting pedicels slender, 8–20 mm long; seeds 1–2 per pyrene, each enclosed in sclerenchyma in the form of a pyrene. Figures 1E, 2B, 15; Jacquin, Icones Plantarum Rariorum 1, t. 46 (as *Solanum lycioides*); Ruiz & Pavon, Fl. peruv. 2: t. 177 (as *Solanum lycioides*); Edward's Bot. Register 32, t. 25. 1846 (as *Solanum lycioides*); Weddel, Chloris Andina 2, t. 55 (as *Solanum lycioides*); Bol. Mus. Paraense Hist. Nat. 4: 603. 1905–1906 (flower, as *Solanum lycioides*). [J. J. Jacquin, 1782. Icones Plantarum Rariorum. 1: t. 46, cites Jacq. Misc. 3.]

Especie con ramas espinescentes y corolas de un azul-violáceo intenso contrastando con el amarillo ladrillo hasta anaranjado de las anteras, bayas deprimido-globosas con 6 pirenos. Su distribución geográfica corresponde exclusivamente al estado Mérida en elevaciones entre 1900 y 3000 m.

Common name. "Cuchuva de Perro."

This species is distinct with its spinescent branches, irregular branching, and small leaves. The corollas are intense blue-violet with a contrasting yellow or brownish eye.

The filaments in our material of this species are not gibbous as recorded by Barboza and Hunziker (1992). *Solanum lycioides* subsp. *parvifolium* (Wedd.) Bitter and *Solanum pseudolycioides* Rusby were considered to be synonyms by Bitter, and we hesitantly consider them to be the taxonomically typical *Solanum lycioides.* Material we have seen has slender, flexuous branching, apparently reflecting young growth rather than a distinct taxon.

Distribution. Uplands of Colombia, Ecuador, Peru, Bolivia, northwestern Argentina, Paraguay, and southern Brazil; in Venezuela in the Andean region. Semi-arid woody formations and remnants, 1900–3000 m elevation. (Map, Fig. 16.) Almost all collections are in flower, and most were made from April to July.

Representative specimens examined. VENEZUELA. **Mérida:** between El Morro & Mérida, 2000–2400 m, *Badillo 6584* (MY); Mucuchíes, 2500 m, *Davidse & Steyermark 18168* (VEN); Quebrada SW of Mucuchíes, 2600 m, *Nee & Whalen 17053* (VEN); Caserío El Vergel between Mucurubá & Mucuchíes, 2900 m, *Ruiz-Terán & López-Palacios 12533* (MERF, MY).

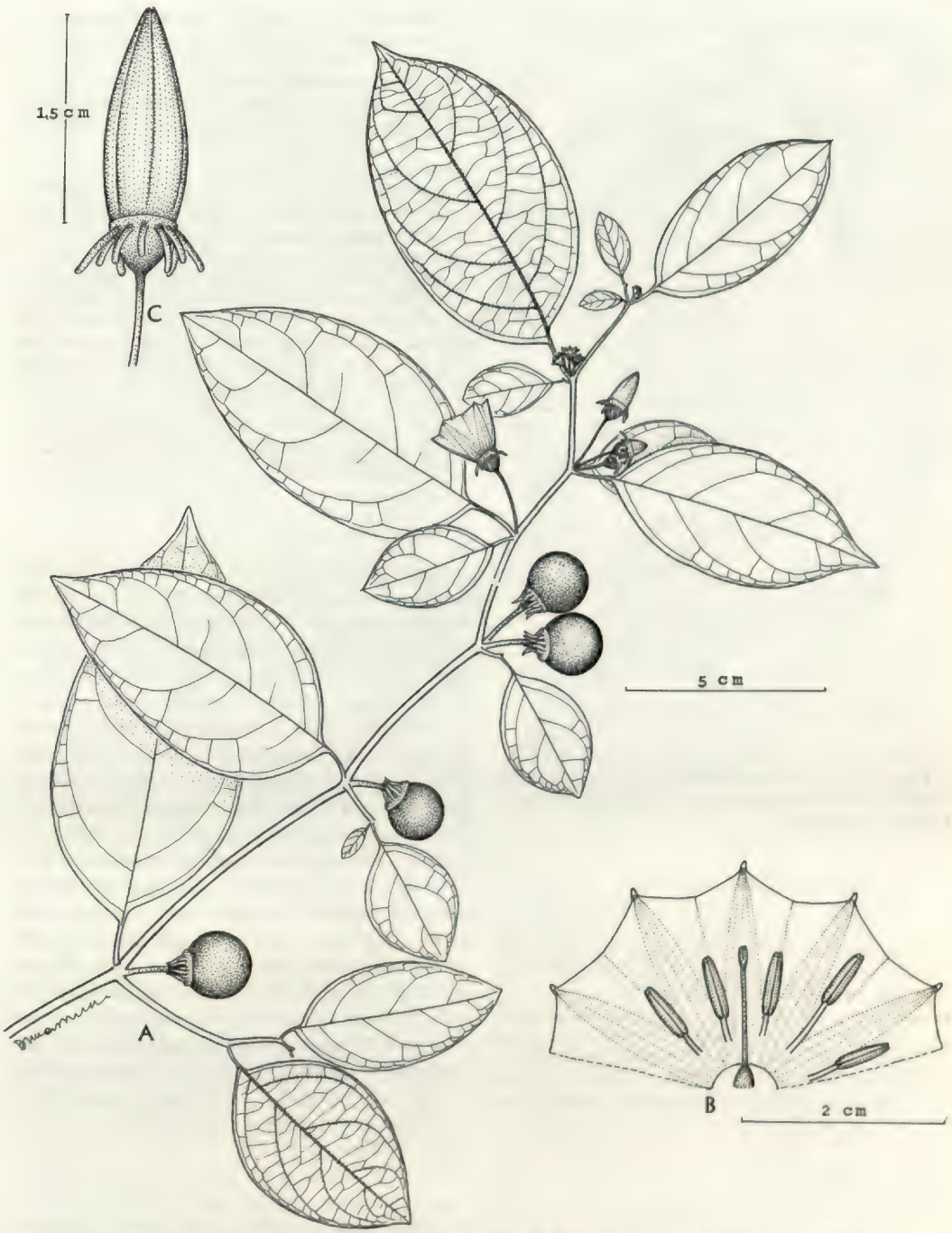

Figure 17. *Lycianthes pauciflora*.—A. Flowering and fruiting branch.—B. Opened flower.—C. Flower bud. After *Steyermark 123694* (MY) and *Trujillo 13947* (MY).

8. Lycianthes pauciflora (Vahl) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 341. 1919 [1920]. Not Sendtn. (1846). *Solanum pauciflorum* Vahl, Eclog. Amer. 1: 20. 1796. TYPE: Martinique (holotype, C-hb Vahl).

Solanum geminatum Vahl, Eclog. Amer. 1: 21. 1797. *Lycianthes geminata* (Vahl) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 392. 1919 [1920]. TYPE: French Guiana. *von Rohr s.n.* (C, = F photo 22887).

Solanum neglectum Dunal, Hist. Sol. 177. 1813. Based on *Solanum arborescens, solani hortensis folio, fructu*

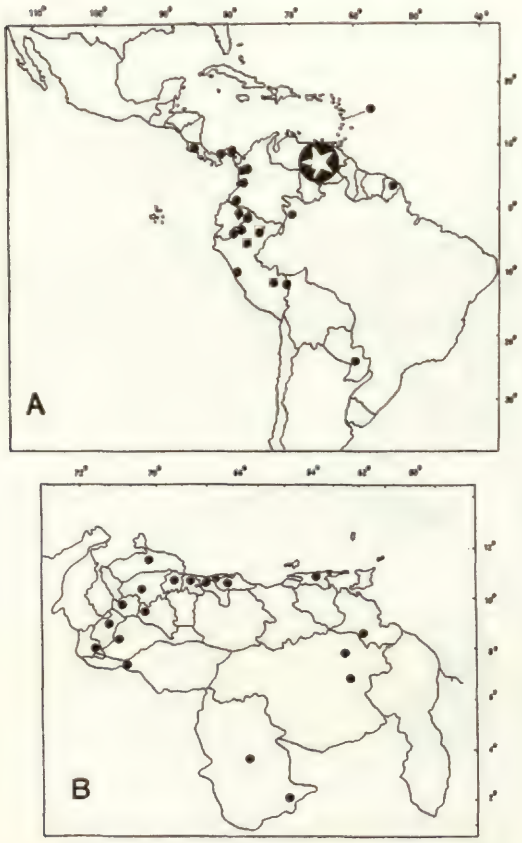

Figure 18. *Lycianthes pauciflora.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

corallino. Maius, Plumier, Pl. Amer. ed. Burmann 242, t. 245, fig. 4. 1760; Plumier, Cat. 4: 34 ined. mss., fide Lourteig (1987). *Lycianthes neglecta* (Dunal) Lourteig, Phytologia 62: 442. 1987. TYPE: Plumier plate based on a plant from Martinique (lectotype, designated by Lourteig (1987)).

Solanum speciosum Dunal, Hist. Sol. 179. 1813. Based on *Solanum arborescens, solani hortensis folio, fructu corallino. Minus,* Plumier, Pl. Amer. ed. Burmann 242, t. 245, fig. 5. 1760; Plumier, Cat. 4: 35 ined. mss., fide Lourteig (1987). *Lycianthes speciosa* (Dunal) Lourteig, Phytologia 62: 442. 1987. TYPE: Plumier plate based on a plant from Santo Domingo (lectotype, designated by Lourteig (1987)).

Solanum sylvaticum Dunal, Solan. Syn. 24. 1816. TYPE: Venezuela. Cumaná, *Humboldt & Bonpland, s.n.* (holotype, P-LA, = IDC 427 microfiche, = F photo, 39015).

Solanum glandulosum Sendtn., in Mart., Fl. Brazil 10: 52. 1846. SYNTYPES: Brazil. Amazonas: Rio Japura, *Martius s.n.* (B destroyed, M not extant, neither seen); southern Brazil, *Sellow* (B).

Solanum japurense Dunal, in DC., Prodr. 13(1): 174. 1852. New name for *Solanum glandulosum* Sendtn., in Mart., Fl. Brazil 10: 52. 1846, non Ruiz & Pavon (1799). *Lycianthes japurensis* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 350. 1919 [1920]. SYNTYPES: Brazil, Rio Negro, Rio Japurá, *Martius s.n.* not seen; southern Brazil, *Sellow s.n.* (B not seen).

Solanum guianense Dunal, in DC., Prodr 13(1): 166. 1852. *Lycianthes guianensis* (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 346. 1919 [1920]. TYPE: French Guiana. Cayenne, *Aublet?* (BM not seen, G-DC not seen, = IDC microfiche).

Solanum urbanum var. *ovatifolium* Chodat, Bull. Soc. Bot. Genève 2(8): 152. 1916. TYPE: Paraguay. Grand forêt de Caaguazu, *Balansa 2080* not seen. [Synonymy of Barbosa & Hunziker (1992).]

Lycianthes pseudolycioides Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 352. 1919 [1920]. New name for *Solanum pseudolycioides* Chodat & Hassler, Bull. Herb. Boissier (ser. 2). 4: 84. 1904. Illegitimate name. Not Rusby (1899). *Solanum australe* Morton, Contr. U.S. Natl. Herb. 29(1): 63. 1944. *Lycianthes australe* (Morton) A. T. Hunz. & Barboza, Darwiniana 31(1–4): 17–34. 1992. Illegitimate combination. TYPE: Paraguay. Arroyo Mocoy, *Hassler 4912* (G not seen, = F photo, 23070, MO, P not seen, = US, photo, Morton neg. 8301).

Solanum caucaense var. *glabrescens* C. V. Morton, Contr. U.S. Natl. Herb. 29(1): 62. 1944. TYPE: Colombia. *Archer 2132* (holotype, US).

High-climbing *shrub* 5–6 m tall, upper branches often dangling and interlocking with other vegetation; branches ferrugineous tomentose, often glabrescent; pubescence of stalked, pauciradiate stellate or dendritic hairs. *Leaves* solitary, ovate, 7–11 × 2–5 cm, apically obtuse or acuminate, basally obtuse or rounded, sometimes oblique, membranous, drying lighter green or brown beneath, veins 3–5 on each side, slightly impressed above, elevated beneath, glabrescent above, softly tomentulose beneath; petioles 0.7–1.6 cm long, tomentose. *Inflorescences* fascicles of 2–5 flowers. *Flowers* crepuscular and nocturnal; pedicels 7–16 mm long; calyx 2–7 × 3–6 mm, sparsely pubescent, teeth 10 in 2 unequal series, sometimes dark purple, later white, 2–6 mm long, reflexed or not; corolla white, rotate, 0.9–2.2 × 1.3–3.5 cm, the margin almost entire, the lobes conspicuously thicker, glabrate; stamens unequal, 4 with filaments 1–2 mm long, the fifth filament 3.3 mm long, anthers 2–5 mm long; ovary ellipsoidal, 1.5–2 × 1–1.5 mm, style 8–9 mm long, exserted 5 mm, stigma capitate. *Berry* bright orange-red, depressed globose or ovoid, 15–20 mm across, stone cells 2–3 or wanting; fruiting calyx accrescent and thickening, 10–14 mm across, the margin sometimes reflexed, the teeth usually reflexed, 3–7 mm long; fruiting pedicels 15 mm long, glabrate; seeds 40–80 per fruit, brown, 2.5–4 × 3.5–4 mm, the thickened margin ca. 0.7 mm wide. Figures 1A, B, D, 2G, 17; Plumier, Pl. Amer. t. 245, figs. 4, 5. 1760; D'Arcy, 1973: 640, fig 13. [Plumier, Pl. Amer. ed Burm. t. 245, fig. 4. 1760. as *Solanum pedunculare alaribus.*]

Es la especie de más amplia distribución geográfica en el país, muy variable en cuanto a grado de pubescencia,

Figure 19. *Lycianthes radiata.*—A. Flowering and fruiting branch.—B. Opened flower.—C. Fruiting calyx. After *Schwartzkoff 12* (MY).

siendo ésta densa y ferrugínea en las ramas jóvenes y floríferas y casi ausente en las ramas adultas y fructíferas, así mismo los dientes del cáliz varían en tamaño desde 2 hasta 6 mm de longitud, siendo reflejos o no en flor y/o en fruto, y el borde puede presentarse reflejo o aplicado; la corola presenta medidas entre 0.9–2.2 cm de longitud y el borde casi entero. Respecto a células pétreas, éstas pueden estar ausentes o en número de 1, 2 ó 4, localizadas en la parte apical interior del fruto.

Common name. "Coronilla."

This species is often seen climbing high in shrubs or low in the canopy and displaying large clusters of showy red fruits. The flowers, usually

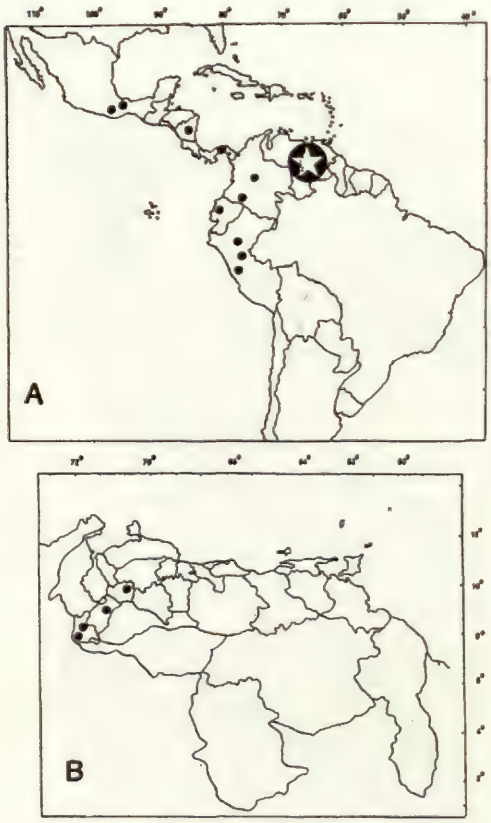

Figure 20. *Lycianthes radiata.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

closed during the day, are less conspicuous. The calyx has conspicuous, porrect, recurved or reflexed, sometimes almost woody teeth.

Distribution. Collections have been seen from Costa Rica, Panama, the Greater and Lesser Antilles, and all tropical countries in South America except Chile and the Guianas, and it probably occurs in the latter region. *Lycianthes pauciflora* is the most wide-ranging species of the genus within Venezuela, and it is variable as to its degree of pubescence and the size and form of its calyx teeth. Cloud forests and gallery forests 600–1500 m elevation. (Map, Fig. 18.) The species appears to flower and fruit throughout the year, but most flowering specimens were collected from April to July and in November and December.

The concept employed here unites concepts of several regional treatments (D'Arcy, 1973; Barboza & Hunziker, 1992) under the oldest name for this wide-ranging species. The Panamanian plants for which D'Arcy used the name *L. guianensis* Dunal have larger fruits and longer, thinner calyx lobes than those from the Antilles, Venezuela, and other eastern parts of the continent, and they may represent a distinct taxon. However, in most particulars, particularly in having fruits with 2 stone cells, the Venezuelan plants agree with the other plants discussed here. Plants of the species from the Antilles, particularly Dominica and Martinique, the type locality of *L. pauciflora*, tend to have slightly smaller calyces and flowers and more rotund leaves than those of Venezuela and the Guianas, but they are otherwise similar. Fruits examined from the Lesser Antilles had varying numbers of stone cells (Martinique, *Duss 364* (US), no stone cells, *Duss 4430* (US), 1 stone cell, Dominica, *Ernst 1942* (US), 2 stone cells). Plants from lowland Paraguay, Bolivia, and Peru have dimensions like those of plants from the Antilles.

Representative specimens examined. VENEZUELA. **Distrito Federal:** between el topo Macanillal & El Pico Izcaragua, 7–12 km E de los tanques de la Electricidad de Caracas, 700–800 m, *Morillo et al. 3272* (VEN). **Amacuro:** Reserva forestal Sierra Imataca, 1988 m, *Sanoja 2002* (MY). **Amazonas:** 5 to 7 km by river E of Cerro La Neblina, 140 m, *Liesner & Funk 15838* (MO, MY, VEN). **Apure:** Reserva Forestal de San Camilo, Chiricoa, 200 m, *Steyermark et al. 101704* (MO, NY). **Aragua:** Carretera Maracay–Choroní, 1200 m, *Benítez et al. 4911* (MY). **Barinas:** Dist. Bolívar, near feldspar mine, between La Soledad and Santo Domingo, 1300 m, *van der Werff & Ortega 6124* (MO, NY). **Bolívar:** El Dorado-La Gran Sabana, 1200 m, *Bunting 2908* (MY). **Carabobo:** Colinas de Guaremales, en la Fortaleza, *Pittier 8803* (VEN). **Falcón:** Sierra de San Luis, S of La Tabla, 1450 m, *Steyermark 98911* (MO). **Lara:** above Sanare toward Las Blanquitas, 1500–1900 m, *Badillo 6687* (MY). **Mérida:** Carretera Estanquez–Las Nieves, 850 m, *Benítez et al. 4826* (MY). **Miranda:** Parque Nacional Guatopo. La Macanilla, 600 m, *Nee 17760* (MO, NY). **Portuguesa:** E of Chabasquen, 1450–1520 m, *Steyermark et al. 126813* (VEN). **Sucre:** Cerro Patao, N of Puerto de Hierro, *Steyermark & Agostini 91324* (VEN). **Táchira:** between Quebrada Grande and El Nula, border with Apure, 250 m, *Gentry & Puig-Ross 14293* (MO). **Trujillo:** Vía Escuque-El Socorro, *Benítez 1952* (MY). **Yaracuy:** Serranía Santa María-Cerro La Chapa, 6 km N de Nirgua, 1200–1350 m, *Meier et al. 3903* (MY, VEN).

9. Lycianthes radiata (Sendtn.) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 433. 1919 [1920]. *Solanum radiatum* Sendtn., in Martius, Fl. Brazil. 10: 53. 1846. TYPE: *Hartweg 1293* [*129* in publication] (BREM not seen, W not seen, B destroyed, = F photo 2586).

Solanum goudoti Dunal, in DC., Prodr 13(1): 158. 1852. *Lycianthes goudoti* (Dunal) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 435. 1919 [1920]. TYPE: Colombia. *Goudot 13* (holotype, G-DC not seen, = IDC microfiche, = F photo, 006772, W not seen).

Lycianthes holocalyx Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 459. 1919 [1920]. TYPE: Ecuador. Provincia Santo Domingo, *Sodiro 114/38* (B destroyed, = F photo 2577)

Figure 21. *Lycianthes sanctaemarthae*.—A. Flowering branch.—B. Flower bud.—C. Opened flower.—D. Infructescence.—E. Seeds. A, B, C. After *Steyermark et al. 122959* (VEN); D, E. After *Bunting 10185* (MO).

Erect or wandlike *shrub* 1–2 m tall, young stems densely pubescent, sometimes glabrescent; pubescence of weak, simple, ascending hairs, those on the internodes to 5.5 mm long. *Leaves* unequal-geminate, major leaves elliptical, sometimes oblique, basally obtuse, the reduced side cuneate, apically acuminate, 10–19 × 3–7 cm, membranous, paler beneath, pilose on both sides, more so beneath, sometimes glabrescent above, veins 7–9 on each side, elevated beneath; minor leaves decurrent on the petiole, 5–9 × 2–3 cm; petioles 0.8–2 cm long, plane above. *Inflorescence* 5–16-flowered. *Flowers* diurnal, a few opening at a time; pedicels 0.6–1.8 cm long, slender, dispersed or densely pubescent with ascending hairs; calyx 2–3.2 mm long and wide, densely pubescent outside,

Figure 22. *Lycianthes sanctaemarthae.*—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

inside with minute, dispersed glands, teeth wanting, the 10 nerves evident, sometimes somewhat elevated; corolla white, rotate, 6–8 mm long, deeply lobed, puberulent outside; stamens equal, filaments 2–2.9 mm long, anthers 2–2.5 mm long, drying with a dark dorsal connective; ovary ovoid, 1.2–1.5 mm long × 0.8–1.3 mm across, style 6 mm long, exserted 3 mm, stigma capitate. *Berry* globose, 5.5–8 mm across, stone cells absent; fruiting calyx slightly accrescent, 2 mm long, mostly strigose; seeds 50–70 per fruit, dark brown, 0.5–1 × 0.75–1.5 mm. Figures 2K, 19.

Esta especie es la única dentro de la Sección *Simplicipila* en Venezuela que no presenta dientes en el cáliz, mostrando 10 nervios conspícuos y un tanto elevados.

This is the only species in section *Simplicipila* in Venezuela that has no teeth on the calyx.

The foliage and pubescence of this species is extremely variable, and the material cited may represent more than one taxon. *Dorr et al. 5104* has smaller, more symmetrical leaves with much less pubescence than the other specimens.

Distribution. Venezuela, Colombia, Ecuador, and Peru. Evergreen forests, 1900–2800 m elevation. (Map, Fig. 20.) The species flowers and fruits throughout the year.

Representative specimens examined. VENEZUELA. **Mérida:** La Mucuy, 1900 m, *Benítez et al. 4185* (F, MO, MY, NY, VEN); E side of Prado Verde-Las Cuadras, 2150 m, *D'Arcy & Benítez 18257* (MO, MY). **Táchira:** 1 km SE of alcabala Páramo El Zumbador, 2750 m, *Pietrangeli 388* (MY). **Trujillo:** between La Playa SW of Carache and Potreritos de Cendé, 2200 m, *Dorr et al. 5104* (MY, NY).

10. Lycianthes sanctaemarthae Bitter, Abh. Naturwiss. Vereine Bremen 24 (1): 377. 1919 [1920]. TYPE: Colombia. Sierra Nevada de Santa Marta, *Smith 1189* (holotype, B not seen; isotypes, CM, F–2, MO).

Shrub climbing to 8 m, young growth tomentose, glabrescent; pubescence of stellate hairs. *Leaves* mostly solitary, ovate, 8–10.5 × 4–8 cm, membranous, paler beneath, veins 3–5 on each side, major veins elevated beneath, both sides with sparse hairs; petioles 1–3 cm long, basally compressed, puberulent; minor leaves ovate, 1.5–2.8 × 1.5–2.5 cm. *Inflorescences* in fascicles of 6–13(–16) flowers; peduncles obsolete or to 10 mm long. *Flowers* with pedicels 11–14 mm long, sparsely pubescent; calyx 3–3.5 × 4–5 mm, sparingly evenly pubescent, drying dark, the margin translucid, teeth wanting; corolla white with a light violet line, the margin sinuate-lobed, the lobes less than ⅓ the length of the corolla, 1.1–1.8 × 2–3.5 cm, evenly dispersed pubescent with simple or stellate hairs; stamens unequal, 4 filaments 1.5–2.2 mm long, the fifth 4–5 mm long, anthers equal, 5–6 mm long, the tips drying discolorous; ovary subglobose, 1.5–2 × 1.5–3 mm, style 10–12 mm long, exserted 2 mm, stigma subcapitate. *Berry* orange, subglobose, 9–12 × 8 mm, stone cells 2, apical in the fruit; fruiting calyx drying uniformly dark brown, 6–8 mm wide, sometimes developing umbos on the sides; fruiting pedicels to 2 cm long; seeds ca. 55 per fruit, yellowish brown, 2–2.5 mm, the thickened margin ca. 0.5 mm wide. Figures 2D, 21.

Presenta el cályx edentado y la pubescencia está representada por tricomas estrellados. Los frutos presentan células pétreas, a diferencia de lo señalado en la literatura en donde en la Sección *Virgatae* a la que pertenece ésta especie, no se mencionan células pétreas.

The calyx of this species lacks teeth and the pubescence is stellate.

Distribution. Restricted to the Sierra Nevada

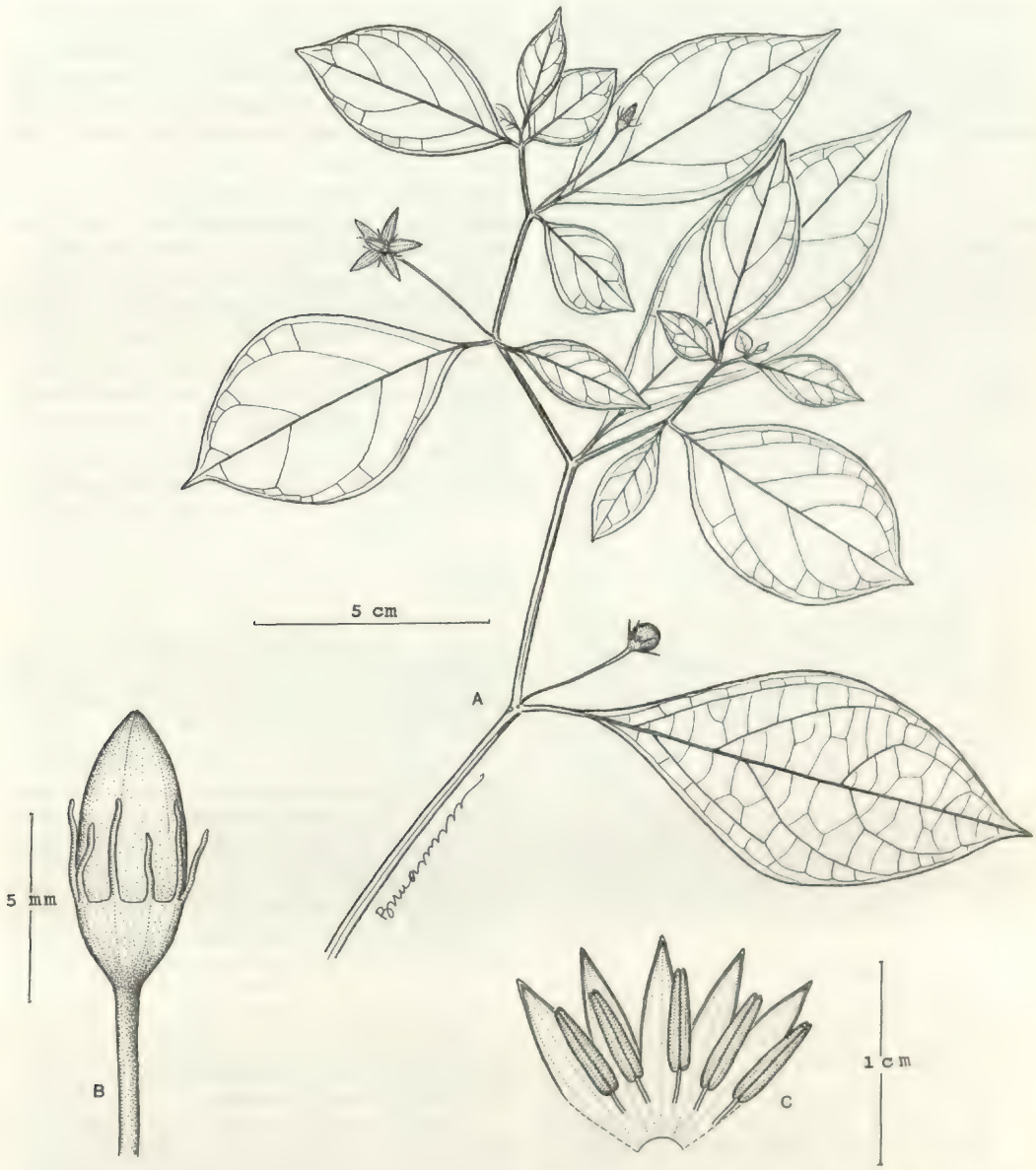

Figure 23. *Lycianthes stenoloba.*—A. Flowering and fruiting branch.—B. Flower bud.—C. Opened flower. After *Mocquerys 978* (MY).

de Santa Marta in Colombia and in the Río Guasare watershed in Zulia State in Venezuela. Riverine forests from 500 to 600 m elevation. (Map, Fig. 22.) We have seen flowering specimens from May and June and fruiting specimens from August.

Although Bitter reported an absence of stone cells in the fruits of this species, we found two in the fruit we examined (*Bunting & Kauffman 10257*).

Representative specimens examined. VENEZUELA. **Zulia:** Dist. Mara, Cuenca de los ríos Socuy-Guasare, en la Paloma, 600 m, *Bunting 10185* (MO), *Bunting & Kauffman 10257* (MO); E of río Guasare, 600 m, *Steyermark et al. 122959* (NY, VEN); Cerro Los Manantiales, E of río Guasare, W of Hacienda Los Manantiales, 600 m, *Steyermark et al. 123281* (NY, VEN).

11. Lycianthes stenoloba (van Heurck & Muell.-Arg.) Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 358. 1919 [1920]. *Solanum stenolobum* van Heurck & Muell.-Arg., Observ.

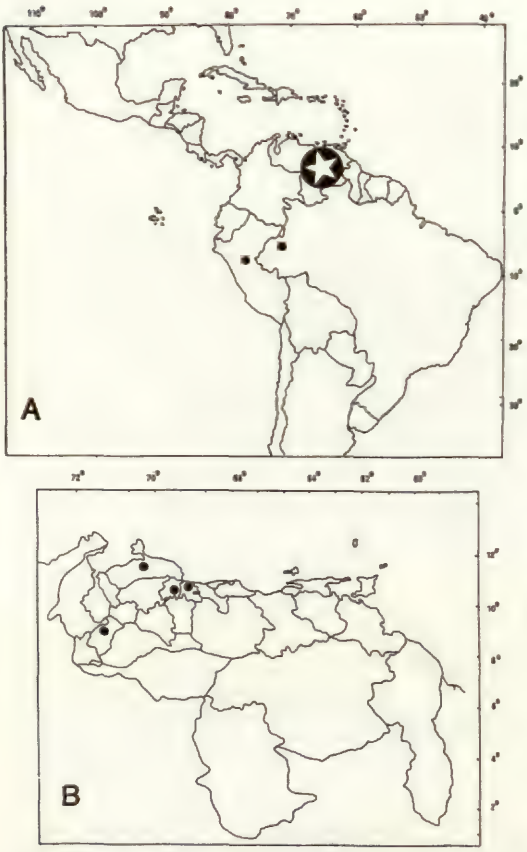

Figure 24. *Lycianthes stenoloba*.—A. Representative distribution outside of Venezuela.—B. Geographic distribution in Venezuela.

Bot. 69. 1870. *Bassovia stenoloba* (van Heurck & Muell.-Arg.) Britton, Mem. Torrey Bot. Club 4(3): 232. 1895. TYPE: Peru. Prope Tarapoto, *Spruce 4210* (G-DC not seen, = IDC microfiche). [A duplicate (syntype) of this collection was cited as being in van Heurck's personal herbarium, but its whereabouts are unknown.]

Lycianthes acutangula Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 357. 1919 [1920]. *Solanum acutangulum* (Bitter) MacBride, Field Mus. Nat. Hist. 13(V-B) 1: 229. 1962. TYPE: Peru. San Govan, *Lechler 2354* (holotype, G, = F photo 23064).

Solanum compressibaccatum (Bitter) Bitter, Repert. Spec. Nov. Regni Veg. 12: 456. 1913. *Lycianthes acutangula* subsp. *compressibaccata* Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 358. 1919 [1920]. TYPE: Peru. *Ule 6800* (B not seen, = F photo 2560 MO, MY).

Lycianthes longidentata Bitter, Abh. Naturwiss. Vereine Bremen 24(1): 356. 1919 [1920]. *Solanum longidentatum* (Bitter) C. V. Morton, Contr. U.S. Natl. Herb. 29(1): 64. 1944. TYPE: Brazil. Rio Acre, Estella, Seringal, S. Francisco, *Ule 9733* (holotype, B destroyed, = F photo 2582; isotype, US).

Sprawling *subshrub* to 4 m tall, internodes 3–6 cm long; pubescence of simple hairs. *Leaves* solitary or geminate, ovate, 9–14 × 3–6.5 cm, apically acuminate, basally cuneate, veins 4–6 on each side, both sides with sparse simple hairs on the main veins, glabrescent, ciliate; petiole 0.5–2 cm long, slightly pilose. Inflorescences 1(–4)-flowered fascicles. Flowers ?diurnal; pedicels slender, very gradually expanding upwards, 1.5–4.5 cm long; calyx 2.5–3 × 1–3 mm, pilose, with 10 subapical, erect, unequal teeth in one series, 2.5–5 mm long; corolla white, rotate or reflexed, lobed ½–⅓ way down, 1–1.5 × 1–2.5 cm, glabrous; stamens mostly unequal, 4 with filaments 0.2–1 mm long, the fifth 0.1–2.5 mm long, glabrous, anthers 4.5–6 mm long; ovary ovoid-conical, style 5–8 mm long, glabrous, exserted 1.5 mm, stigma bilobed. Berry orange, compressed-ovoid, 9 × 8 mm, sometimes with 2 stone cells; fruiting calyx 8.5 mm long; seeds ca. 24 per fruit, yellowish brown, 3 × 2 mm. Figures 2H, 23.

Esta especie es conspícua por la longitud de sus pedicelos florales cuyas medidas oscilan entre 1.5–4.5 cm de longitud y la corola presenta el borde lobado, con lobos de longitud ½–⅓ de la longitud de la corola.

This species can be recognized by its slender, often wide-flaring calyx teeth, its usually elongate, slender usually arching pedicels, and its anthers held tightly together in a cylinder. The corolla is conspicuously lobed.

"*Solanum acutangulum* Griseb." appeared as a nomen nudum in Lechler, Berberid. Amer. Austral. (58. 1857).

Distribution. Venezuela, Brazil, and Peru. Deciduous woods and semi-deciduous riversides, 200–700 m. (Map, Fig. 24.) Collected in flower and fruit from June to September.

Lycianthes stenoloba is much like the following species from Central America: *Lycianthes guatemalense* Bitter, *Lycianthes stephanocalyx*, (J. S. Brandeg.) Bitter, and *Lycianthes solitarium* (Blake) Standl. The Central American species were treated in part by Gentry and Standley (1974) and Dean (1995), and Nee (1986) treated *Lycianthes stephanocalyx* for Veracruz, Mexico. The name *L. stenoloba* is employed for this species with hesitation. In the original description and in the type photos and other material seen for the synonyms cited, the calyx is mostly longer—4–9 mm as opposed to 2–3 mm—than in the Venezuelan material. Bitter reported finding two stone cells in fruits of this species, but we found none in the fruits we examined.

Representative specimens examined. VENEZUELA.

Carabobo: Valle Seco, camino hacia La Toma, 100–200 m, *Benítez & Pons 4654* (MY). **Falcón:** Sierra de San Luis, between Santa Lucía and Cabure, 800 m, *van der Werff & B. Vera 864* (CORO, MY). **Mérida:** El Vigia, *Macqueys 978* (MY, P). **Yaracuy:** Finca Antonia, San Felipe, *Ferrari 791* (MY).

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List of Species

1. *Lycianthes acutifolia* (Ruiz & Pavon) Bitter
2. *Lycianthes amatitlanensis* (Coult. & J. D. Smith) Bitter
3. *Lycianthes asarifolia* (Kunth & Bouché) Bitter
4. *Lycianthes ferruginea* Bitter
5. *Lycianthes inaequilatera* (Rusby) Bitter
6. *Lycianthes lenta* (Cav.) Bitter
7. *Lycianthes lycioides* (L.) Hassler
8. *Lycianthes pauciflora* (Vahl) Bitter
9. *Lycianthes radiata* (Sendtner) Bitter
10. *Lycianthes sanctaemarthae* Bitter
11. *Lycianthes stenoloba* (van Heurck & Muell.-Arg.) Bitter

Collections of *Lycianthes* from Venezuela Studied

Specimens are listed alphabetically by collector, followed by collector number and herbarium of deposit; the species is indicated by a number in parentheses corresponding to the number in the text and in the List of Species.

Adamo s.n. (MERC) (7). Agostini 3 (VEN) (8). Agostini et al. 1701 (VEN) (11). Allart 318-2 (NY, VEN) (1). Aristeguieta 1749 (NY, VEN) (8); 3994 (MO, VEN) (6); 4233 (MO, NY, VEN) (1); 7122 (NY) (1). Aristeguieta & Foldats 1406 (VEN) (3). Aristeguieta & Pannier 1973 (VEN) (3).

Aymard & Flores 216 (MY, PORT, VEN) (7). Aymard et al. 1643 (MY, PORT) (8); 2839 (MY, PORT) (3).

Badillo 1816 (MY) (6); 1914 (MY) (8); 4426 (MY) (8); 5672 (MY) (4); 6584 (MY) (7); 6636 (MY) (8); 6687 (MY) (4). Badillo & Holmquist 6217 (MY) (8). Badillo et al. 7841 (MY) (8). Benítez 318 (MY) (6); 517 (MY) (3); 683 (MY) (7); 1181 (MY) (8); 1335 (MY) (8); 1353 (MY) (8); 1408 (MY) (4); 1418 (MY) (1); 1446 (MY) (4); 1551 (MY) (1); 1554 (MY) (6); 1562 (MY) (8); 1952 (MY) (8); 2068 (MY) (4); 2243 (MY) (8); 2614 (MY) (6); 3214 (MY) (6); 3621 (MY, NY) (3); 3868 (MY) (1); 3869 (MY) (4); 3898 (MY) (1). Benítez & Otero 4609 (MY) (1). Benítez & Pons 4651 (MY) (3); 4654 (MY) (11). Benítez & Rojas 3087 (MY) (8); 3993 (MY) (3); 5000 (MY) (8). Benítez et al. 3221 (MY) (3); 4184 (MY) (7); 4185 (F, MO, MY, NY, VEN) (9); 4235 (MY) (4); 4236 (MY) (1); 4259 (MY) (3); 4261 (MY) (8); 4611 (MY) (9); 4847 (MY) (9); 4884 (MY) (8); 4911 (MY) (8); 5104 (MY) (4); 5117 (MY) (4); 5129 (MY) (4); 5148 (MY) (4). Bernardi 433 (MER) (1); 1834 (VEN) (1); 2327 (NY, MER) (8); 5687 (NY) (8); 5792 (MER, NY) (3); 5930 (MER) (8). Berry 940 (VEN) (4); 944 (VEN) (1). Bianco 39 (CAR, VEN) (3); Bianca 302 (MER, MO, VEN) (8). Bonpland 71 (P) (6). Breteler 3628 (MER, VEN) (1). Bunting 2908 (MY) (8); 3020 (MY) (8); 4433 (MY) (6); 5808 (VZU, MO, VEN) (6). Bunting 10185 (MO) (10). Bunting & Kauffmann 10257 (MO) (10); Burkart 16324 (VEN) (6).

Cárdenas 4038 (MY) (8). Castillo 1930 (MY) (9). Carnevali et al. 614 (MY, VEN) (8). Cesari (VEN-249120) (1). Colonello 930 (CAR) (8). Croat 54841 (VEN) (5). Cumana 1850 (IRBR, MY) (6).

D'Arcy & Benítez 18257 (MO, MY) (9). Davidse 4035 (VEN) (4). Davidse & Steyermark 18168 (VEN) (7). Davidse & González 18899 (NY, VEN) (5); 21914 (NY) (8). Davidse & Miller 27476 (MO, MY) (8). Delascio 51 (CAR) (3); 122 (CAR) (1); 981 (CAR) (4); 9026 (CAR) (4). Delascio & de Delascio 2692 (CAR, VEN) (3). Delascio & López 12838 (MO, VEN) (3). Demey (CORO, MY-86695) (4). Diederichs 173 (VEN) (4); 177 (VEN) (8); 270 (VEN) (8); 279 (VEN) (8). Dorr & Barnett 7183 (MER, MO) (8). Dorr et al. 4749 (MY, NY) (8); 5104 (NY, VEN) (9); 5263 (NY) (7). Duno et al. 184 (MY) (6).

Edwards et al. 94 (MY) (8).

Fendler 974 (MO, P) (1); 991 (G, MO, NY) (4); 1065 (NY) (3). Fernández, A. 379 (MY) (3); 497 (MY) (6); 606 (MY) (8); 620 (MY) (8); 1112 (MY) (8); 3697 (MY) (1); 3762 (MY) (8); 3963 (MY) (8); Fernández, F. 98 (VEN) (8). Ferrari 733 (MY) (8); 790 (MY) (3); 791 (MY) (11); 859 (MY) (7).

Gentry & Puig-Ross 14293 (MO) (8). Gentry & Stein 47275 (MO, MY, VEN) (8).

Humbert 26108 (MER, P) (1); 26156 (MER, P) (1). Humboldt 748 (P) (6).

Ijjasz & Madriz 164 (MY, VEN) (7).

Jahn 1211 (VEN) (6); 1248 (VEN) (6). Jeffrey & Trujillo 2510 (MY) (8).

Knapp & Mallet 6766 (BH, MY) (2); 6807 (BH, MY, VEN) (1).

Lasser 1068 (VEN) (4); 1203 (VEN) (4); 2044 (VEN) (8); 2212 (VEN) (8). Licata et al. 32 (MY, PORT) (3). Liesner 10038 (VEN) (1); 12833 (MY, VEN) (5). Liesner & Funk 15838 (MO, MY, VEN) (8). Liesner & González 9732 (VEN) (8); 9773 (VEN) (2); 9969 (VEN) (8). Liesner & Guariglia 11631 (MO, NY, VEN) (8). Liesner et al. 7803 (MY, MO, VEN) (3). Linden 437 (G) (4); 478 (P) (3). López-Figueiras & Rodriguez 9080 (MERF) (7). López-Palacios 1457 (MERF, MO, MY) (7); 1539 (MO) (4); 2206 (MERF, MY, VEN) (8). López-Palacios & Bautista 3485 (MER) (8).

Magallanes (MY-9313) (6). Manara (MY-83285) (11); (VEN-71770) (3); (VEN-176544) (3). Marcano-Berti 1409 (MER) (8). Marcano-Berti & López-Palacios 1758 (MER, MY) (4). Marcano-Berti & Carrillo 29-4-78 (MER) (8). Mocquerys 880 (P, VEN) (6); 978 (MY, P) (11); s.n. (P) (6). Montaldo 3756 (MY) (8). Morillo 2519 (VEN) (2); 3384 (VEN) (1); 11148 (MERF, MY) (7). Morillo & García 11472 (MERF, MY) (1). Morillo & Manara 1600 (MY, VEN) (1); 2022 (VEN) (3); 2070 (MY) (3). Morillo & Seres 8614 (VEN) (1). Morillo & Smith 6057 (MY, VEN) (4). Morillo et al. 2940 (VEN) (8); 3272 (VEN) (8). Moritz 1642 (G, P) (4).

Nee 31048 (MO, MY, NY, VEN) (8). Nee & Whalen 16899 (MO, NY) (8); 17053 (VEN) (7); 17146 (NY, VEN) (3); 17760 (MO, NY) (8). Nilsson & Steyermark 221 (VEN) (8).

Ortega 892 (VEN) (3).

Pannier 199 (MERF, VEN) (5). Pefour 6 (MERC) (7). Peñaloza 205 (CAR) (1). Pietrangeli 338 (MY) (9); 1331 (MY) (9). Pittier 5972 (NY) (3); 8803 (VEN) (8); 9129 (NY, US, VEN) (3); 9378 (NY, VEN) (1); 10036 (VEN) (1); 10057 (NY, VEN) (1); 11179 (VEN) (6); 11867 (MO, NY, VEN) (8); 13088 (MO, NY, VEN) (6); 13237 (MO, NY, VEN) (7); 13514 (MO, VEN) (4). Pittier & Nakichenovich 15543 (VEN) (8). Plowman 7766 (P, MO, NY) (1). Plowman et al. 13445 (NY) (8). Poelt & Oberwinkler 14991 (VEN) (7).

Quintero 2173 (MER) (9). Quintero & Hernández 246 (MER) (9).

Ramírez 2071 (MY) (4). Ricardi 1093 (MERC) (1). Rodríguez, G. 770 (MY, VEN) (9); Rodríguez, H. 74 (MY) (3). Rodríguez et al. 1346 (MY) (1). Rodríguez & Cardozo 1712 (MY) (1). Romero 486 (MY) (6); 854 (MY) (8). Rosales 11 (MY, VEN) (4). Ruiz-Terán 645 (MER) (8); 2128 (MERF) (1); 8802 (MERF) (7). Ruiz-Terán & López-Figueiras 64 (MERF, MY) (1); 245 (MER, MERF, MY) (7). Ruiz-Terán & López-Palacios 6708 (MERF) (7); 11470 (MERF, MY) (8); 12533 (MERF, MY) (7).

Saer 118 (VEN) (6); 263 (NY, VEN) (3). Sanoja, E. 2002 (MY) (8). Schnee 830 (MY) (4). Schwarzkopf 12 (MERF, MY) (9); 48 (MY) (1). Smith V1341 (MY, UCOB) (1); V4464 (MY, UCOB) (8); V4465 (VEN) (4); V4466 (VEN) (4); V7557 (MY, VEN) (4). Smith V9384 (MY) (8). Sobel et al. 2062 (NY) (3). Stein & Gentry 1512 (MO, MY, VEN) (8). Stergios & Aymard 4451 (MY, PORT) (3). Stergios et al. 6360 (MY, PORT) (5). Steyermark 55405 (MY, VEN) (1); 55945 (MY, VEN) (4); 56015 (MY) (1); 56262 (VEN) (7); 56494 (NY, VEN) (4); 56628 (F, MY, VEN) (9); 56632 (VEN) (4); 56939 (MY, VEN) (4); 56957 (VEN) (4); 57433 (MY, VEN) (4); 60971 (MY, VEN) (3); 86204 (NY, VEN) (4); 87105 (VEN) (8); 89040 (VEN) (8); 89896 (NY, VEN) (8); 89951 (NY, VEN) (8); 90991 (VEN) (8); 91601 (NY) (1); 98911 (MO) (8); 99013 (VEN) (8); 102180 (MO, NY, VEN) (6); 106197 (MO, NY, VEN) (8); 106473 (MO, NY) (1); 115464 (MO, VEN) (4); 119551 (MO, VEN) (8); 120002 (VEN) (8); 121528 (VEN) (2); 121593 (VEN) (2); 121927 (VEN) (1); 126813 (VEN) (8); 126823 (VEN) (8). Steyermark & Agostini 91324 (VEN) (8). Steyermark & Davidse 116492 (VEN) (3); 116662 (VEN) (8). Steyermark & Espinoza 105842 (VEN) (8). Steyermark & Liesner 118330 (VEN) (9); 118386 (MO, VEN) (9); 119186 (VEN) (8); 120743 (VEN) (8); 120772 (MO, NY, VEN) (2). Steyermark & Manara 110995 (MO, NY, VEN) (6); 125326 (VEN) (1). Steyermark & Mass 123694 (MY, VEN) (8). Steyermark & Stoddart 118046

(VEN) (8). Steyermark & Steyermark 95433 (VEN) (3). Steyermark & Rabe 96125 (P, VEN) (2); 96718 (VEN) (8). Steyermark & Wessels-Boer 100481 (MO, NY, VEN) (8). Steyermark et al. 92969 (VEN) (8); 98795 (MY, VEN) (4); 100742 (MY, VEN) (1); 101704 (MO, NY) (8); 102599 (VEN) (8); 104542 (VEN) (8); 105798 (MO) (8); 109926 (VEN) (3); 110242 (MY, VEN) (4); 122959 (NY, VEN, VZU) (10); 123500 (MO, VEN) (1); 124590 (MY, VEN) (3); 124685 (MY, VEN) (8); 124991 (VEN) (3); 126679 (VEN) (8); 127216 (MY, VEN) (3). Suarez & Gil 53 (MER) (7).

Tamayo 283 (VEN) (6); 397 (VEN) (4); 1229 (VEN) (1). Trujillo 1260 (MY) (4); 2917 (MY) (1); 3325 (MY) (3); 5237 (MY) (8); 6358 (MY) (7); 13947 (MY) (8); 15829 (MY) (8); 15967 (MY) (3). Trujillo & Bunting 7598 (MY) (1). Trujillo & del Castillo 8265 (MY) (1). Trujillo & Fernández 362 (MY) (1); 368 (MY) (1); 372 (MY) (1); 10597 (MY) (3). Trujillo & Ponce 19715 (MY) (3). Trujillo et al. 16574 (MY) (6); 16662 (MY) (6).

van der Werff 4767 (VEN) (8); 4811 (VEN) (8); 5453 (VEN) (8); 6124 (MO, NY) (8). van der Werff & Vera 864 (CORO, MY) (11). Velasquez 110 (CAR) (8); 310 (CAR) (1).

Whetzel & Muller 485 (VEN) (1). Williams 10269 (VEN) (8); 10789 (VEN) (8); 11084 (MY, VEN) (3). Wingfield 12989 (CORO, MY) (11). Wood 448 (VEN) (3). Wood & Berry 85 (VEN) (1).

Xena 626 (MY) (4).

Index to Scientific Names

Asaropsis
lenta 182
Section 171
Bassovia 182
inaequilatera 182
stenoloba 196
Boldoa 179
repens 179
Brachistus 182
inaequilaterus 182
Capsicum 167, 170
Jaltomata 170
Lycianthes
lenta 171
acapulcensis 172
acutangula 196
acutangula subsp. compressibaccata 196
acutifolia 171, 174
amatitlanensis 171, 172, 175
armentalis 182
asarifolia 171, 172, 177, 179
australe 190
candicans 187
conicibaccata 171
ferruginea 171, 172, 180, 182
geminata 189
goudoti 192
goudotii 171
goudotii var. uberior 174
guatemalense 196
guianensis 190, 192
holocalyx 192
inaequilatera 171, 172, 176, 182
japurensis 190
jelskii 182
lehmannii 174
lenta 171, 172, 184
lenta var endopsila 185
lenta var. scotinophila 185
longidentata 196
lycioides 168, 170–172, 186
lycioides subsp. tomentosa 187
lysimachioides 171
moziniana 171
pauciflora 168, 171, 172, 182, 185, 189, 190, 192
pseudolycioides 190
radiata 171–173, 192
rantonnei 171
repens 178, 179
sanctaemarthae 171, 194
Section 171
Section Asaropsis 171
solitarium 196
stenoloba 171, 195, 196
stephanocalyx 171, 196
Subgenus 171
subsect 172
ulei 176
ulei subsp. dolichodonta 176
ulei var. strigulosa 176
variifolia 171, 186
xylopiifolia 174
xylopiifolia var. intermedia 174
Meiomeris
series 172
Oligochondra
series 171
Otilix 172
Pachystemonum
sect. 172
Physalis 170
Polymeris
Section 171
Subgenus 171
Simplicipila
Section 171, 194
Solani
hortensis folio, fructu corallino 189, 190
Solanum
acutangulum 196
acutifolium 174
amatitlanense 176
asarifolium 177, 178
australe 190
candicans 186
caucense var. glabrescens 190
chodatianum 178
compressibaccatum 196
cumanense 184
declinatum 184
geminatum 189
goudoti 192
guianense 190
japurense 190
lambii 184
lentum 184
lentum var. echinatum 184
longidentatum 196
lyciiforme 187
lycioides 167, 172, 186
lycioides subsp. parvifolium 188
lycioides var. tomentosa 186
neglectum 189

nocturnum ... 184
pauciflorum ... 189
phillyreoides ... 187
pseudolycioides ... 187, 188, 190
quadriflorum ... 184
radiatum ... 192
sect. Lycianthes ... 171
sect. Pachystemonum subsect. Lycianthes ... 172
series Meiomeris ... 172
speciosum ... 190
stenolobum ... 195
subgenus Lycianthes ... 172
sylvaticum ... 184, 190
urbanum var. ovatifolium ... 190
violaefolium ... 180
violaefolium fo. lilaciniflora ... 178
violaefolium var. majus ... 177
violiifolium var. asarifolium ... 177
violiifolium var. asarifolium fo. decadontum ... 178
violiifolium var. majus fo. chacoense ... 178
virgatum ... 184
virgatum var. lentum ... 184
xylopiaefolium ... 174
Triguera ... 170
Virgatae
Series ... 171
Witheringia ... 170

DIALYPETALANTHUS FUSCESCENS KUHLM. (DIALYPETALANTHACEAE): THE PROBLEMATIC TAXONOMIC POSITION OF AN AMAZONIAN ENDEMIC[1]

Frederic Piesschaert,[2]
Elmar Robbrecht[3] *and Erik Smets*[2]

ABSTRACT

The neotropical rainforest tree *Dialypetalanthus fuscescens* Kuhlm. is the only species of the Dialypetalanthaceae. In-depth morphological and anatomical documentation is presented, including newly recorded features such as indeterminate inflorescences, anthers with calcium oxalate packages, silica bodies in the wood, U-shaped placentas and dendritic hairs, and corrections of erroneous literature observations, e.g., on supposed stipular dimorphism. The genus is heterobathmic, combining advanced gynoecial characters with such primitive features as free petals, dimery, stipules, and (here postulated) cantharophily. In the past, *Dialypetalanthus* was most frequently suggested to be related to Myrtales or Gentianales. However, because of the lack of bicollateral vascular bundles, presence of well-developed stipules, paracytic stomata, obvious endosperm and unitegmic ovules, seed-coat structure, and gynoecial origin of the disk, a close relationship with the Myrtales is unlikely. An affinity with the Gentianales, the Rubiaceae in particular, is accepted instead. It is concluded that ontogenetic and micro- and macromolecular data are much needed for a further elucidation of the relationships of *Dialypetalanthus*.

The monospecific Amazonian genus *Dialypetalanthus* is enigmatic as regards its systematic position. Characters such as the opposite, entire leaves with sheathing stipules and the dry fruits with winged seeds obviously point to a position in (or near) the Rubiaceae. However, a close relationship with the Rubiaceae must be questioned because of the presence of certain deviant floral characters (e.g., free petals and numerous stamens in two whorls with their filaments fused into a basal ring). As for the classification of *Dialypetalanthus*, all present authors accept its familial status, but they do not agree about the relatives of the Dialypetalanthaceae. While some prefer a position in the Myrtales or Rosales, others assign the family to Gentianales or Rubiales. In the present paper we aim (1) to document knowledge of *Dialypetalanthus fuscescens* Kuhlm. as broadly as possible and (2) to clarify its systematic position.

HISTORICAL SURVEY

In October 1874, Ferreira was the first to collect some flowering branches of a yet unknown tree from the Amazonian region. The specimen (*Ferreira 438*) was filed in the herbaria of K and LISU as an unidentified taxon of the Rubiaceae. In 1925 the tree was re-collected and described by Kuhlmann as the new genus and species *Dialypetalanthus fuscescens* Kuhlm.

According to Kuhlmann (1925, 1942), the ascending imbricate ovules, winged seeds, and embryo "formando núcleo central" (1942: 25) clearly indicate a relationship between *Dialypetalanthus* and Rubiaceae, more specifically with the tribe Cinchoneae of the subfamily Cinchonoideae sensu Schumann (1891). Kuhlmann established a monogeneric tribe Dialypetalantheae in the Rubiaceae, characterized by free petals and anisomery.

After a reinvestigation, mainly of wood and leaf anatomical characters, Rizzini and Occhioni (1949) established the monotypic family Dialypetalanthaceae. They concluded that the Dialypetalanthaceae are to be placed in the Myrtales, somewhere near the Myrtaceae (*Eugenia*), Melastomataceae (*Huberia*), or Hydrocaryaceae (= Trapaceae). Note that

[1] We are grateful to Steven Jansen for preparing the wood sections, to L. Macias and P. Delprete for providing additional distribution data, to the directors of the herbaria of K, NY, L, and US for providing herbarium specimens, to Marcel Verhaegen for the preparation of SE-micrographs of pollen, and to Johan Buelens for making photographs of herbarium specimens. This research was supported by the Fund for Scientific Research-Flanders (F.W.O., Belgium, project G.0143.95).

[2] Laboratory of Plant Systematics, Botanical Institute, K.U.Leuven, Kardinaal Mercierlaan 92, B-3001 Heverlee, Belgium.

[3] National Botanic Garden of Belgium, Domein van Bouchout, B-1860 Meise, Belgium.

Kuhlmann (1925) had already mentioned that the copious flowering of *Dialypetalanthus* reminded him of certain Myrtaceae. In addition, Rizzini and Occhioni sent samples of *Dialypetalanthus* to some "eminent botanists" (Burkart, Erdtman, Lam, Janssonius, and Bremekamp), asking for their opinion. In 1952, Occhioni and Rizzini assembled their answers into a publication. All the taxonomists consulted accepted the establishment of a new family, which probably explains why it is generally accepted today. They disagreed, however, about its possible relatives. Burkart stated that relatives of *Dialypetalanthus* should be looked for somewhere in his Myrtiflorae; Erdtman concluded that the pollen of *Dialypetalanthus* resembles that of certain Rhizophoraceae (see also Erdtman, 1971); Lam, while admitting some resemblances to the Rubiaceae, suspected a relationship with Lythraceae or Melastomataceae; Janssonius found similarities between the wood of *Dialypetalanthus* and that of the genus *Psychotria* of the Rubiaceae; finally, Bremekamp agreed with Rizzini and Occhioni (1949) that relatives of *Dialypetalanthus* should be sought near the Myrtaceae and Melastomataceae, notwithstanding the large leaf-like stipules and lack of intraxylary phloem (see also Bremekamp 1966: 3, 8).

Emberger (1960), Melchior (1964), Cronquist (1968), Stebbins (1974), and Dahlgren (1975) followed Rizzini and Occhioni (1949) and placed the Dialypetalanthaceae in the Myrtales. Cronquist (1981), however, reconsidered his opinion, placing *Dialypetalanthus* in "the rather amorphous Rosales" (p. 551), where it was kept in his system of 1988. He refused to associate the family either with Myrtaceae (because of the stipules and the lack of internal phloem) or with Rubiaceae (because of the free petals and numerous stamens on top of the ovary).

Dahlgren also changed his view on the systematic position of *Dialypetalanthus*. At first, he transferred the Dialypetalanthaceae from Myrtales to Cornales (Dahlgren, 1980); later he moved the family to Gentianales (Dahlgren, 1983; no arguments were provided for this transfer, but are presumably the same as given in Dahlgren & Thorne, 1984; discussed further).

According to Hutchinson (1959), free petals and polyandry occur in Dialypetalanthaceae, as well as in some genera of the Rubiaceae, and should not be considered as distinctive characters (but his argument does not hold; see Discussion). He placed the Rubiaceae and Dialypetalanthaceae in a separate order Rubiales, closely related to the Loganiaceae (Gentianales).

In a study of the Myrtales, Dahlgren and Thorne (1984) concluded that *Dialypetalanthus* should be excluded from the order. Stressing inter alia the paracytic stomata, they considered the Dialypetalanthaceae as an "early off-shoot of the Rubiaceae or a relict family closely related to the Rubiaceae in the Gentianales" (p. 690).

Robbrecht (1994), in a review of the delimitation of the Rubiaceae, added a few new characters that are in common between Dialypetalanthaceae and Rubiaceae, namely the thickening pattern of the inner tangential walls of the exotestal cells and the occurrence of colleters on the adaxial surface of the stipules. He concluded that a profound study of the Dialypetalanthaceae is needed to shed more light on the possible relationships.

In their consensus classification of the Gentianales, Nicholas and Baijnath (1994) suggested that *Dialypetalanthus* represents an archaic group without any close living relatives. They excluded the genus from the Gentianales and placed it near the order Cornales and its allies, concluding that it needs much closer analysis.

Material and Methods

This study is based on herbarium material from NY, US, and K (herbarium abbreviations following Holmgren et al., 1990). Numerous attempts to obtain fixed material were unsuccessful. The distribution map was completed with locality data from specimens from the Museu Goeldi (MG) (data provided by L. Macias, Belém).

Both for scanning electron microscopy (SEM) and light microscopy (LM) observations, the herbarium material was prepared by simple boiling or by the method described by Peterson et al. (1978), using a mixture (6:1) of 10% aqueous di-(2-ethylhexyl) sodium sulfosuccinate, and 98% acetone for 24 hours (see also Erbar, 1995). For LM, the material was dehydrated in an alcohol series and embedded in paraffin, using a Histokinette 2000. Sections (10–14 μm) were made with an M1R Shandon rotation microtome, and subsequently colored with safranin (10 min) and fastgreen (4 min) in a Varistain 24-3, Shandon. After staining, the sections were mounted in Eukitt. Observations were made with a Dialux 20 Leitz microscope.

For SEM, the material was dehydrated in an alcohol series and FDA (formaldehydedimethylacetal). After critical-point drying (CPD 030 Critical Point Dryer, Balzers), the material was mounted on stubs with Leit-C Conductive Carbon Cement and sputter-coated with gold (± 180 nm) in a Spi-module® Sputter Coater (Spi Supplies). Observations were made with a JEOL JSM-6400 electron micro-

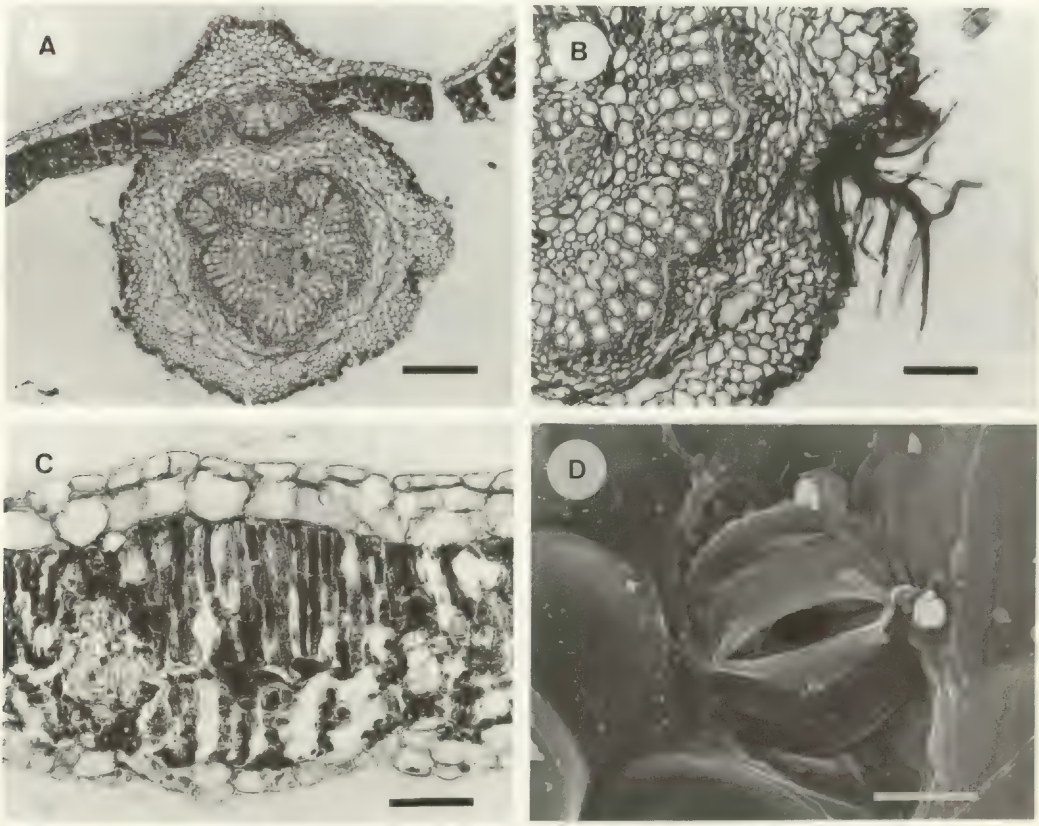


Figure 1. Leaf structure of *Dialypetalanthus fuscescens.* (A–C LM; D SEM.)—A. Transverse section of the main vein; bar = 0.25 mm.—B. Dendritic hair on the main vein; bar = 0.1 mm.—C. Transverse section of the lamina; bar = 50 μm.—D. Paracytic stoma in surface view; bar = 10 μm. After *Cid Ferreira 9018* (A–C) and *Lobo et al. 328* (D).

scope. In order to show the thickenings of the inner tangential walls of the exotestal cells, the outer tangential walls had to be removed. Therefore, boiled seeds were transferred to a 3:1 mixture of alcohol 96% and acetic acid 99% for 24 hours. Afterward they were put in a 3% aqueous mixture of sulphuric acid at 50°C for at least 10 hours (modified from Braune et al., 1967). Remaining specks of dirt were removed by ultrasonication.

The methods used for acetolysis and breaking pollen grains are discussed in detail by Huysmans et al. (1994). Wood anatomical sections were prepared as described by Jansen et al. (in prep.).

Results

Vegetative Structures

Habit. *Dialypetalanthus fuscescens* is a large, slender rainforest tree reaching up to 30 m (but usually smaller). It has a soft, fibrous (because of the formation of several concentric phellogen layers), red to cinnamon-colored bark. The trunk is fluted toward the base. The wood is light but extremely hard. It is used locally for house construction (Rizzini & Occhioni, 1949), but as far as we know it has little economic value.

Leaves. The simple leaves are decussately arranged and have blades with entire margins. The petiole is well developed (0.6–3.5 cm) and shallowly sulcate above. The blades are broadly elliptic (L/W-ratio 1.5:1), elliptic (2:1), suborbiculate (1.2:1), to narrowly (2:1) or widely obovate (1.2:1) (sometimes slightly asymmetric), with a shortly acuminate to rounded tip, and an obtuse, acute or cuneate to slightly decurrent base (terminology following Hickey, 1988); they are (2–)6–17(–20) × (1–)4–11(–14) cm. The leaf venation is pinnate and camptodromous. The veins, especially the midvein (Fig. 1A), are prominent on the abaxial side of the blade. The divergence angle between primary and secondary veins is about 35° in the center of the blade and gradually rises toward the base of the leaf. The veins are detectable up to the fifth order.

The areoles have a more or less constant shape and size. The leaves become gradually smaller and have a lower L/W-ratio toward the inflorescence region, and are eventually replaced by bracts. The petiole and veins are densely covered with unicellular to uniseriate hairs on the abaxial side. Dendritic hairs occur as well very sporadically (Fig. 1B). The adaxial side of the leaf is almost completely glabrous or bears few hairs along the main veins. Domatia are absent. The upper epidermis consists of flat, rectangular cells (Fig. 1C) that occasionally contain crystals of an unknown nature. The strongly developed cuticle runs over the leaf margin and gradually becomes thinner on the lower epidermis. The outer tangential wall of the epidermal cells is straight, except above the veins, where it is rounded. Beneath the upper epidermis, a well-developed hypodermis occurs with clearly larger cells. The palisade tissue is well developed and consists of a maximum of 6 cell layers (often less). It is interrupted only by the main veins. At the leaf margin, the palisade tissue is replaced by angular collenchyma. According to Rizzini and Occhioni (1949), the spongy mesophyll and palisade tissue are separated by a layer of isodiametric cells (not seen by us). The lower epidermis (inclusive of the hypodermis) is much thinner and more irregular than the upper epidermis. The difference in cell size between epi- and hypodermis is much less pronounced. Stomata are paracytic, randomly oriented, more or less sunken, and found only in the lower epidermis (Fig. 1D). The vascular configuration of the petiole and midvein is complex and rather variable in successive sections (Fig. 1A). In the center, short radial vessel rows are arranged in an arc, open toward the adaxial side. The main leaf anatomical characters were described by Rizzini and Occhioni (1949). Most of their observations were confirmed in our preparations.

Stipules. At each node, two large leaf-like stipular lobes—the most conspicuous vegetative character of *Dialypetalanthus*—occur on either side between the two petioles (Fig. 2). Rizzini and Occhioni (1949), Hutchinson (1959), and Cronquist (1981) considered them to be intrapetiolar, while Dahlgren and Thorne (1984) described them as interpetiolar. We observed that the four stipular lobes are connected at their base to form a low sheath around the stem, i.e., they are intra- as well as interpetiolar. This sheath is covered adaxially with a basal row of long silvery hairs and colleters of the standard Rubiaceae type (that is, consisting of an axis of elongated cells, covered by a palisade-like epidermis; Robbrecht, 1988). The abaxial surface is densely covered with unicellular to uniseriate trichomes. Rizzini and Occhioni (1949) claimed that *Dialypetalanthus* has two types of stipules, namely normal and "bud stem covering" ones ("bud stipules" as we will call them in the following discussion). They considered this so-called "stipular duality" to be unique in the dicotyledons. The bud stipules would bear a "remarkable pilose scale at the base" and fall off when the "gemma" (apical bud) increases. We have dissected several intact terminal buds (Fig. 3A), looking for possible scars of former structures, but could not confirm the findings of Rizzini and Occhioni. After we had removed the outer stipules (these are the bud stipules of Rizzini and Occhioni) of a terminal bud, two structures, densely covered with hairs, indeed appeared (Fig. 3B, C). However, their position (alternating with the last normal pair of leaves and alternating with the hairy structures of the next node; Fig. 3D), and their clearly pinnate venation pattern, proves that these "pilose scales" are reduced leaves. Therefore, there is no essential difference between bud stipules and the other stipules. The only genuine stipular dimorphism we noticed is in the transition zone between vegetative and generative parts, i.e., at the base of the inflorescence. Here consecutive nodes bear stipules that differ strongly, mainly

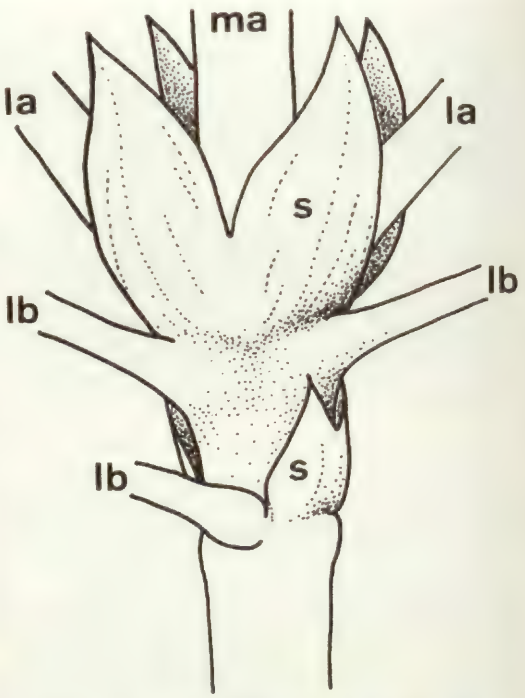
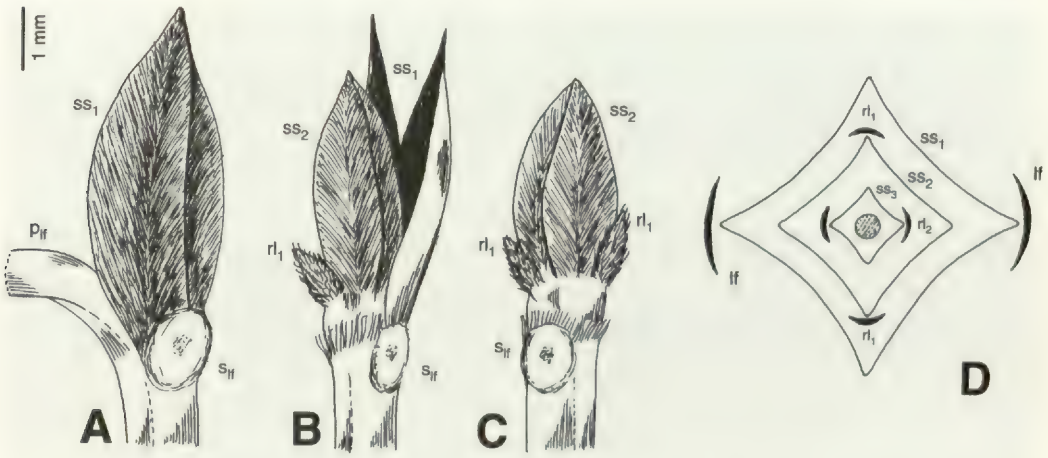


Figure 2. Stipular dimorphism at the base of an inflorescence; lb = leaf base, s = stipule, la = lateral inflorescence axis, ma = main inflorescence axis.



lf: leaf (s_{lf}, scar of leaf; p_{lf}, petiole); rl_1, rl_2: reduced leaves; ss_1, ss_2, ss_3: stipular sheaths

Figure 3. Dissection of a terminal vegetative bud of *Dialypetalanthus fuscescens*.—A. Intact bud.—B. Half of the outer stipular sheath removed, revealing a reduced hairy leaf and the stipular sheath of the next node.—C. Outer stipular sheath removed completely.—D. Schematic representation of a vegetative bud. After *Nee 34472*.

in size (upper ones much larger than the short, triangular lower ones; Fig. 2). Anatomically, the stipules have a characteristic adaxial epidermis, consisting of thickened cells. Scattered through the homogeneous chlorenchyma are numerous small vascular traces that are surrounded by fibers. Rizzini and Occhioni (1949) recorded occasional paracytic stomata in the abaxial epidermis.

Wood anatomy. The wood of *Dialypetalanthus* shows indistinct growth rings (probably reflecting the precipitation cycle), marked by a transition from thin- to thick-walled fibers. The fibers are septate (Fig. 4C) and have simple pits in vertical rows (Fig. 5D) (libriform fibers sensu Baas, 1986). The wood is diffuse-porous. The vessels are solitary or arranged in short radial rows (2–8 cells) (Fig. 4D, E). In young wood, close to the pith, the radial vessel rows are often longer. The outline of the solitary vessels is rounded (Fig. 4E), although the smaller vessels are often compressed between the larger ones. Axial parenchyma is present and occurs as scanty, paratracheal strands (Fig. 4B). The width of the rays varies from (1–)2 to 6 cells (Fig. 4A); their height may exceed 100 cells. In radial sections, the procumbent body-ray cells have a margin of one or often several layers of square cells (Fig. 4F). Sometimes a mixture of procumbent and more or less square cells occurs. The rays are visible to the naked eye as clear, narrow, parallel lines. The pith and the rays contain very small cubic to prismatic crystals; navicular crystals occur as well. The septate fibers as well as the rays contain silica-bodies (Fig. 4G, H). The perforation plates of the vessels are simple, bearing a single elliptical to almost circular opening (Fig. 5A). The vessel-ray pits are simple (Fig. 5B). The intervessel pits are alternately arranged and vestured (Fig. 5C). Internal phloem is absent.

REPRODUCTIVE STRUCTURES

Inflorescence. The bloom of *Dialypetalanthus* is copious, with numerous white, fragant flowers in large inflorescences. The inflorescence of *Dialypetalanthus* (Figs. 6–8) was described by Kuhlmann (1925) as paniculate and racemose. Rizzini and Occhioni (1949) and Hutchinson (1959) also indicated it was a panicle. According to Weberling (1992), a panicle is characterized by terminal flowers on its main axis and side branches. Thus, a panicle is a determinate inflorescence. *Dialypetalanthus*, however, does not have a terminal flower but a terminal bud that at first sight may be confused with a single terminal flower. Dissection of the terminal bud reveals a floral meristem where acropetal inception of lateral flowers occurs (the flowers in the most terminal zone seem to be poorly developed) (Fig. 7). The inflorescence of *Dialypetalanthus* is thus indeterminate, contrary to a panicle. Dahlgren and Thorne (1984) provided the first correct illustration of the inflorescence but did not describe it. Cronquist (1981) was the first to correctly call the *Dialypetalanthus* inflorescence a thyrse. More specifically, it is a frondobracteose, heterothetic, indeterminate thyrse with opposite branches (Fig.

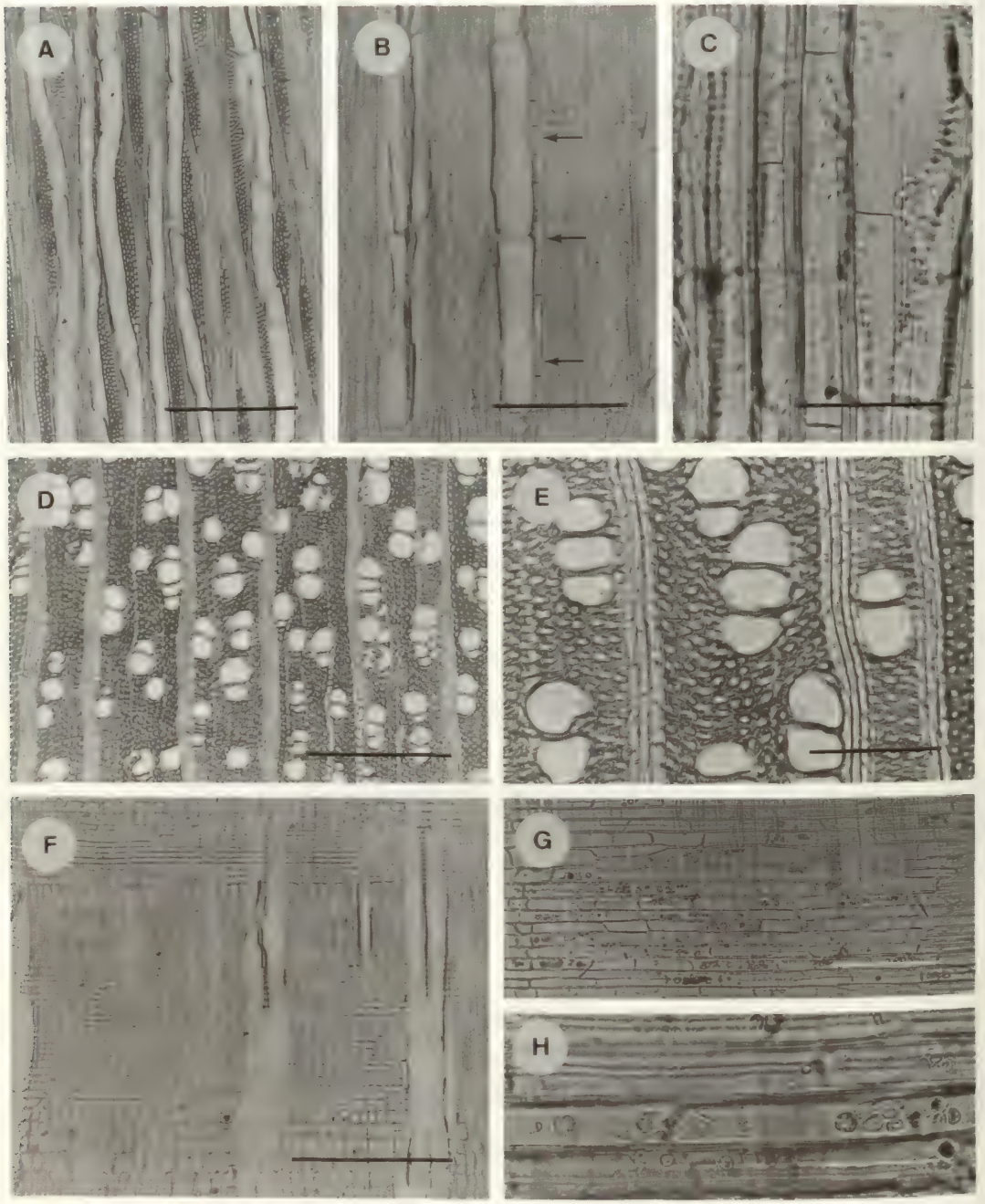


Figure 4. Wood anatomy of *Dialypetalanthus fuscescens* (LM).—A. Tangential section; bar = 0.5 mm.—B. Radial section showing paratracheal parenchyma (arrows); bar = 0.35 mm.—C. Tangential section of septate fibers; bar = 50 μm.—D, E. Transverse sections with short radial vessel rows and 4-cellular rays; bars: D = 0.5 mm, E = 0.2 mm.—F. Radial section of a ray with several layers of square marginal cells; bar = 0.5 mm.—G. Radial section showing silica bodies in a ray; bar = 0.2 mm.—H. Radial section with detail of silica bodies; bar = 50 μm.

8) (all terms sensu Weberling, 1992). The inflorescences are (usually) terminal. Normally, two side branches occur at each node (three branches in the type specimen, *Kuhlmann 1514*; observed nowhere else). Bracteoles are situated somewhere near the middle of the pedicel. The bracts, bracteoles, and true leaves of the inflorescence are all deciduous. As mentioned earlier, the transition zone from

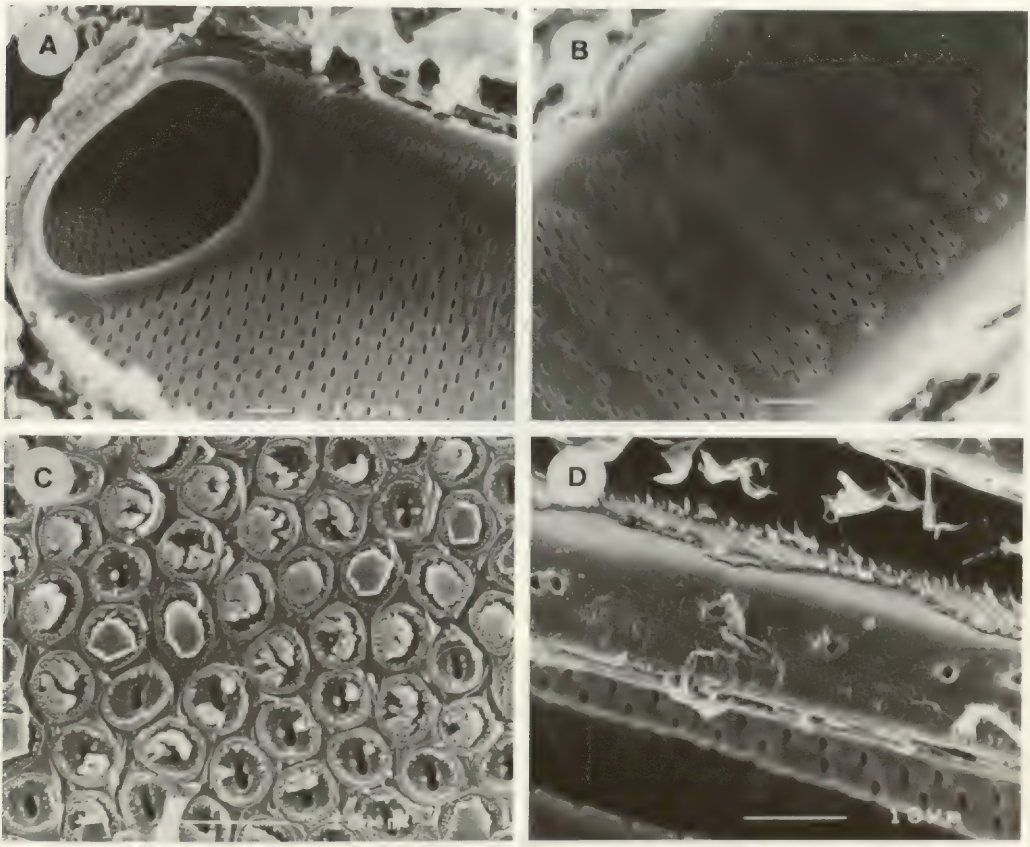


Figure 5. Wood anatomy of *Dialypetalanthus fuscescens* (SEM).—A. Simple perforation of a vessel.—B. Simple pits between a vessel and underlying ray parenchyma.—C. Vestured pits.—D. Simple fiber pits.

woody to herbaceous parts at the base of the inflorescence is characterized by a short stem portion with different-sized stipules.

Calyx. The calyx of *Dialypetalanthus* consists of four green, semicircular lobes. These lobes arise as two decussate whorls of two primordia (Fig. 9G). In early ontogenetic stages, the sepals cover the other floral structures completely (cryptopetaly sensu Sprague, 1940). Later, they are pushed apart by the developing petals, stamens, and style. The abaxial side of the sepals as well as that of the petals is covered with a typical, velvet-like indumentum, consisting of long uniseriate hairs, with the exception of a rather broad (1 to 2 mm) hairless border. The margins are fringed. Apart from the base, the adaxial side of the sepals is glabrous. As in the other floral structures, the sepal lobes are thick and fleshy. In the center, they usually consist of about 20 cell layers. The cells of the epidermis are clearly smaller than the cells of the underlying parenchyma. Numerous vascular traces occur in the center of the parenchyma. The sepal lobes are persistent. During maturation and dehiscence of the fruit, they are split in two (Fig. 15A).

Corolla. The corolla is composed of four free, white petals. Just like the calyx lobes, they arise as two decussate whorls of two primordia each (Figs. 9G, 10). This dimerous origin of calyx and corolla (sometimes noted in the literature: Cronquist, 1988; Maas & Westra, 1993) should be represented on a floral diagram with petals opposite to sepals (Fig. 10), instead of alternating with them. In very young buds, all petals are globular and cover almost completely the interior floral parts. In older stages, petals enclose the interior floral parts in pairs. During anthesis, the petals unfold into broadly elliptic (2 to 2.5 cm long and 1.5 cm wide), shortly ungulate structures. The innermost petal is distinguished from the other petals because of an apical prolongation with transparent hairs at the margin in the bud stage. The inner petals are often more or less wrinkled, thus allowing rapid expansion during anthesis. Aestivation is imbricate, but with variations. Sometimes a petal will overlap an-

Figure 6. Flowering specimen of *Dialypetalanthus fuscescens* with flowers in late bud stage (*Fernández Casas & Susanna 8188,* NY); bar = 5 cm.

other on both sides, as is always the case with the inner petal whorl (and the sepals); sometimes the overlapping will occur only on one side (this has only been observed in the outer petal whorl). As mentioned above, the abaxial indumentum of the petals is comparable to that of the calyx lobes. The adaxial side is glabrous. The corolla is shed shortly after anthesis (Fig. 9D). It is not clear whether pollination has already occurred at that stage or if the yellow-colored stamens take over the attractive function of the corolla. Anatomically, the corolla is very similar to the calyx. The fleshy petals have a distinct epidermis with relatively small cells. Beneath the epidermis there is a poorly differentiated, many-layered parenchyma enclosing numerous, parallel vascular bundles. Crystal sand occurs scattered through the parenchyma.

Androecium. The androecium of *Dialypetalanthus* consists of 16 to 25 (usually less than 20; commonly 16 or 17) stamens that are united at their base into a short androecial ring atop the ovary, free from the corolla. Two whorls can be distinguished within the androecium, the outer whorl always having more stamens than the inner. A slight dimorphism can be seen between stamens of the two whorls: the inner ones have slightly longer anthers and a shorter filament than the outer ones (Fig. 9A). The stamens are closely packed together in bud stage and tightly enclose the developing style. They

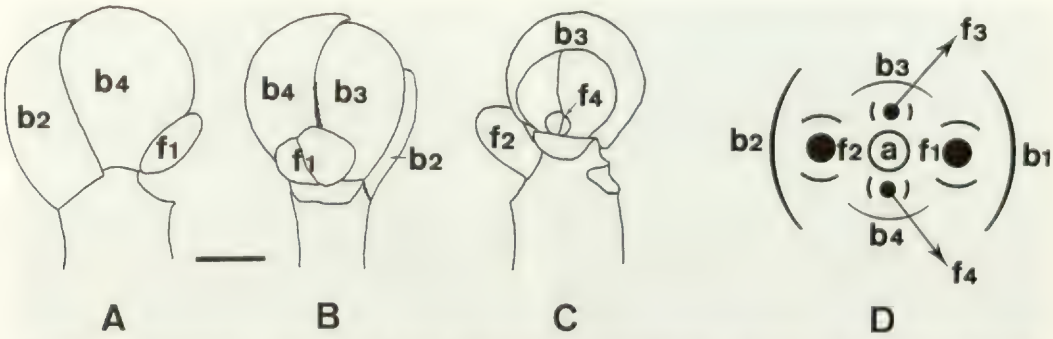


Figure 7. Dissection of a terminal bud of the inflorescence of *Dialypetalanthus fuscescens*.—A. Right bract removed, revealing the right floral bud surrounded by two bracteoles (f1).—B. The same dissection showing a frontal view of the two bracteoles around the right floral bud.—C. Same view as A; left bract (b2), right floral bud (f1), and bract of the next whorl (b4) also removed, showing left floral bud of the first whorl (f2) and floral bud of the second whorl (f4).—D. Schematic representation of a terminal inflorescence bud; a = axis; bar = 1 mm. After *Ducke 22816*.

are yellow-green and remain after the corolla has fallen off. Later, the androecium falls off as a whole, leaving only the style.

Each locule consists of two clearly separated pollen sacs (Fig. 9B). The locules are large, elongate (7 to 8 mm long and 2 mm wide), and pointed to the lateral-adaxial side. The short filament (Fig. 9A) is basifixed and continues in a massive, essentially abaxial connective (Fig. 9B). A peculiarity of the stamens of *Dialypetalanthus* is the (very) sporadic occurrence of stellate trichomes on the anthers (Fig. 9E). In most cases, however, the stamens are completely glabrous. The locules possess two horn-like appendages at their apex (Fig. 9C). These locular appendages are curved toward each other and have two basal branches, one to each pollen sac (Fig. 11A). Kuhlmann (1925) did not mention these structures at first, but later he called them, rather unfortunately, "little valves" (Kuhlmann, 1942). Neither Rizzini and Occhioni (1949), Hutchinson (1959), nor Cronquist (1981) paid any attention to these appendages; Dahlgren and Thorne (1984) illustrated them but did not refer to them. The locular appendages are clearly visible in bud stage (Fig. 11A). Just before anthesis the anthers tear open between the basal branches of the appendages (Fig. 11B), leaving small, more or less round pores at the top of the locules (Fig. 11C) through which the pollen is released. Anther dehiscence therefore is porate (as stated by Kuhlmann, 1925; Rizzini & Occhioni, 1949; Cronquist, 1981; Dahlgren & Thorne, 1984). It has to be mentioned, however, that in some cases the pollen sacs are split open over their entire length, probably explaining why Hutchinson (1959) stated that dehiscence is longitudinal. The locular appendages consist of parenchymatic tissue filled with crystal sand, surrounded by a more or less sclerified zone (Fig. 9C). A similar kind of calcium oxalate accumulation in anthers was described for Solanaceae and some other families by D'Arcy et al. (1996). They reported a special type of hypodermal tissue in the stamens, the so-called resorption tissue, filled with calcium oxalate crystals and situated at the stomium, running lengthwise around the anther. During maturation of the stamens, the tissue surrounding the

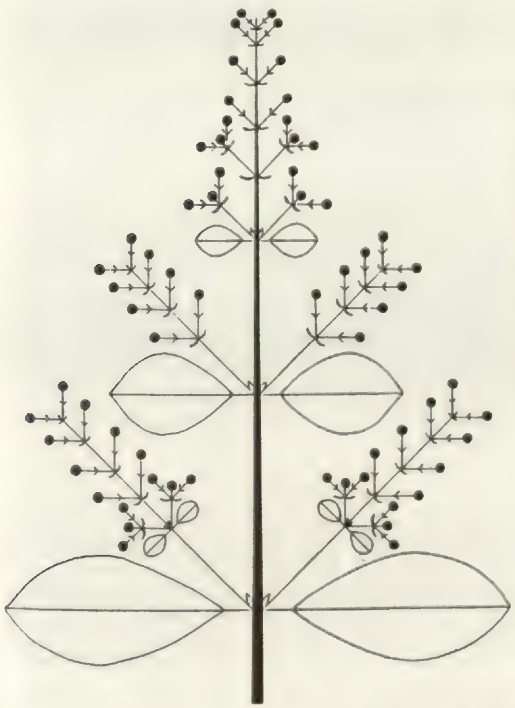


Figure 8. Schematic representation of the inflorescence of *Dialypetalanthus fuscescens*.

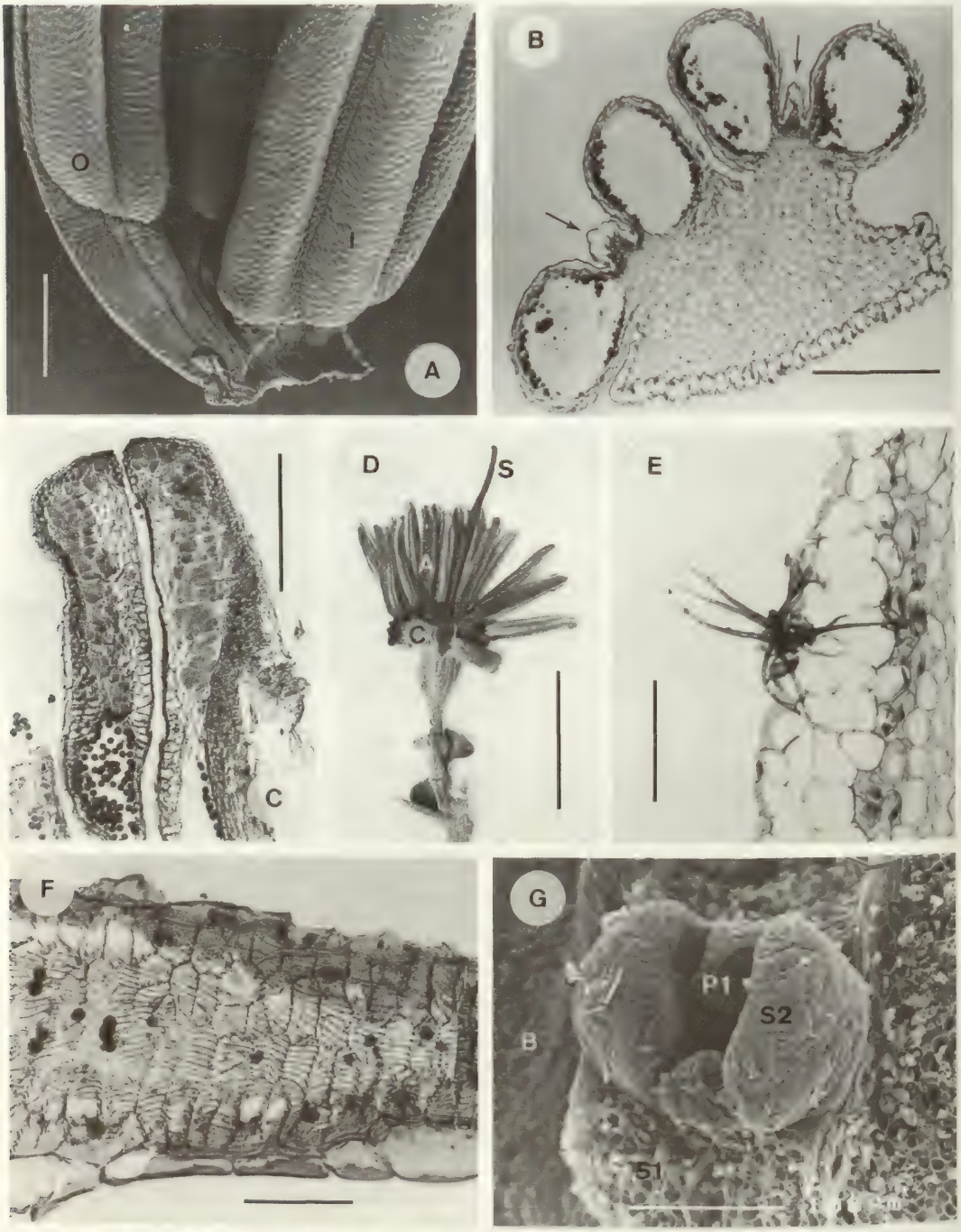


Figure 9. Androecial structure (A-F) and floral ontogeny (G) of *Dialypetalanthus fuscescens*. (A and G SEM; B, C, E, and F LM; D macro photograph.)—A. View of the fused base of the outer (O) and inner (I) androecial whorls; bar = 1 mm.—B. Transverse section of a stamen; note the epidermal protuberance between the pollen sacs (arrows); bar = 0.5 mm.—C. Longitudinal section of the crystalline appendix of a locule; bar = 0.25 mm.—D. Appearance of a flower after the petals have fallen off; S = style, A = androecium, C = calyx; bar = 1 cm.—E. Stellate hair on stamen; bar = 0.25 mm.—F. Endothecial thickenings; bar = 0.1 mm.—G. Young flower showing the dimerous origin of calyx and corolla; B = whorl of bracts, S1 = first sepalous whorl, S2 = second sepalous whorl, P1 = first petalous whorl. After *Ducke 22816* (B, C, E, F, G), *Ducke 21684* (A), and *Nee 34472* (D).

Figure 10. Floral diagram of *Dialypetalanthus fuscescens*. Note the alternation of dimerous whorls. The stamens are united at their base into a short androecial ring.

resorption tissue disintegrates and a mass of crystals, the "oxalate packages" (O.P.'s), is set free. It appears that the situation in *Dialypetalanthus* is very similar, although the location of the crystals (at the top of the anthers instead of the stomium) is somewhat different (see also the section on Pollination Biology). Various possible functions (e.g., in anther dehiscence, discouragement of herbivores, as pollinator reward) for the O.P.'s were discussed by D'Arcy et al. (1996), but the exact role of these structures remains unclear.

The inside of the pollen sacs is covered with small (< 1 μm), globular, smooth orbicules. Huysmans et al. (1997) have recently drawn attention to these easily overlooked structures in Rubiaceae. Between the pollen sacs of each locule, a clear epidermal protuberance with remarkably enlarged epidermal cells occurs (Fig. 9B). The same epidermal configuration is found in between the locules, at the adaxial side of the connective. In transverse sections, the cortex cells of the connective are isodiametric with large intercellular cavities. Longitudinally, the cells are elongated and clearly smaller than the epidermal cells. They become smaller in the proximity of the pollen sacs. The cortex zone beneath the epidermal protuberances is strongly lignified, often with off-shoots into the endothecium (Fig. 9B). A one-layered endothecium occurs, except at the dorsal side of the pollen sacs. The endothecial thickenings are mostly spiral, seldom circular or U-shaped, or may even be absent (Fig. 9F). In longitudinal sections the endothecial cells have the polygonal appearance of cambial cells, with their longitudinal axis perpendicular to that of the cortical cells. The well-developed connective is triangular in cross section (Fig. 9B). It contains one central vascular bundle that seldom splits into two smaller bundles at the apex of the stamens. In the filament, at the adaxial side of the vascular bundle, one can find a half circle of dark-staining cells, possibly with high metabolic activity. A transverse section of the androecial ring shows a ring of dark-colored cells connecting the vascular bundles of all stamens. The function of these cells is unclear.

It is not yet clear how the androecium is initiated. Most probably it is not an example of primitive polyandry (that is, each stamen arising as a separate primordium; Ronse-Decraene & Smets, 1992), but a case of complex polyandry. In view of the dimerous origin of calyx and corolla, we expect the existence of two alternating whorls of two complex primordia each, giving rise to numerous stamens by "dédoublement." This would also be in

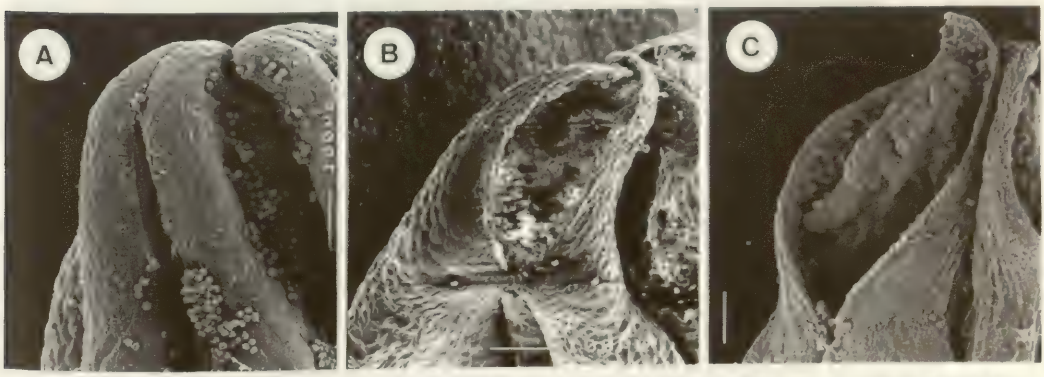


Figure 11. Appendages of the anthers of *Dialypetalanthus fuscescens* (SEM).—A. Locular appendage before anthesis.—B. Stage between A and C: appendage tears open between its basal branches.—C. Locules after anthesis; the appendages are completely torn open. After *de Albuquerque et al. 1295* (A), *Ducke 22816* (B), and *Anderson 11865* (C).

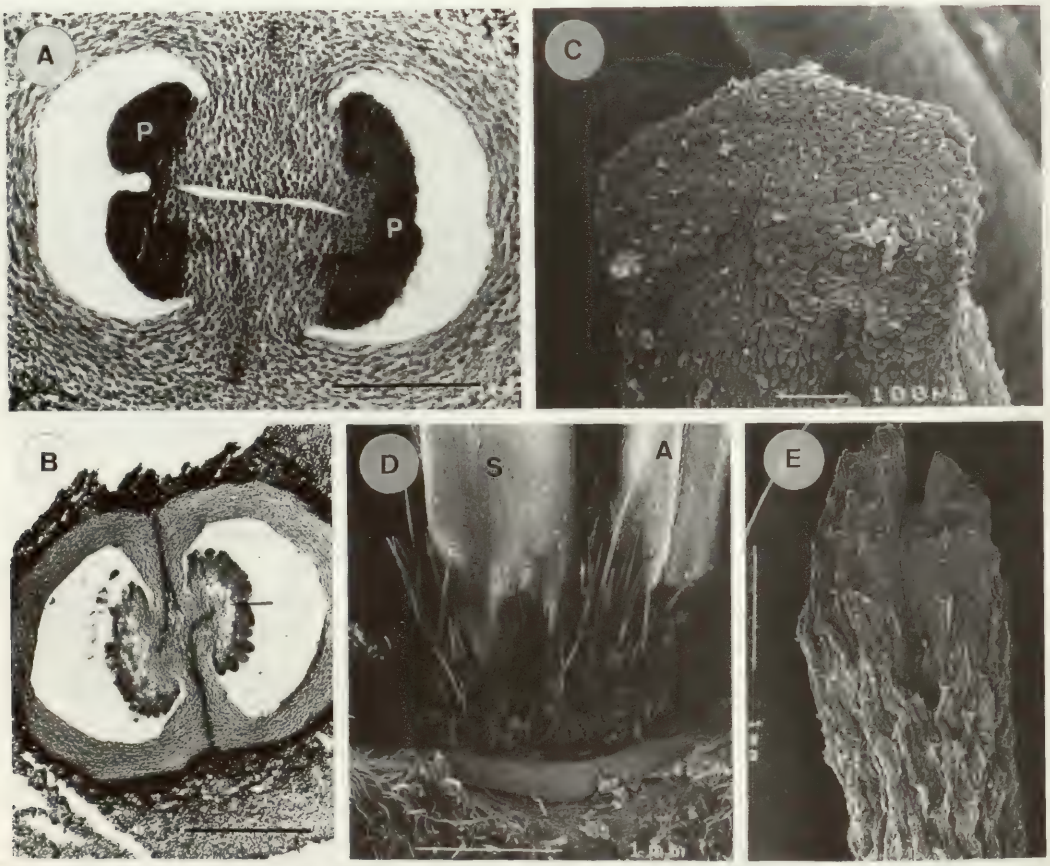


Figure 12. Gynoecial structure of *Dialypetalanthus fuscescens*. (A, B LM; C–E SEM.)—A. Transverse section at the top of a young gynoecium; P = placental zone; bar = 0.2 mm.—B. Transverse section of mature gynoecium, seen with polarized light; note the uplighting oxalate crystals in the placenta (arrow); bar = 0.5 mm.—C. Slightly bilobed, papillose stigmatic surface.—D. Long hairy disk at the base of the style (S); A = anther.—E. Apical split of the placenta in fruit stage. After *Vilhena et al. 1003* (A), *Nee 34518* (B), *de Albuquerque et al. 1295* (C), *Ducke 21684* (D), and *Thomas et al. 5205* (E).

accordance with the alternation pattern of dimerous whorls in the flower as a whole.

Pollen. The pollen of *Dialypetalanthus* is trizonocolporate (Fig. 13A). The grains are oblate-spheroidal in equatorial view (P/E-ratio 0.88–1) and rounded to triangular in polar view. The polar diameter (P) varies from 17 to 21 μm, the equatorial diameter (E) from 19 to 24 μm. The margins of the ectocolpus are irregular, but form sharp angles at the end (Fig. 13B). The mesoaperture is a porus or colpus (2 to 3 μm long and mostly less than 1 μm wide), often provided with a clear margo or annulus (Fig. 13B). The endocolpus (Fig. 13E) is oriented perpendicular to the exocolpus; it has the same dimensions as the exocolpus but is more regularly bordered. The ends of the endocolpi are sometimes bifurcate (Fig. 13F). The apocolpium is well-developed (apocolpium-index 0.35–0.45; Fig. 13A, C). The sexine is tectate perforate (perforations < 1 μm; muri larger than lumina but still < 1 μm; Fig. 13C, D). Muri are smooth to warty. The inside surface of the pollen grains is granular between the margins of the endocolpi (Fig. 13F, white star). At the top of the endocolpi, the endexine is characterized by a weak-looking zone with many irregular grooves that connects the endocolpi (Fig. 13F, black star). Sexine is as thick as or slightly thinner than the nexine (Erdtman, 1971). The columellae are short and thick.

Gynoecium. The inferior ovary of *Dialypetalanthus* is composed of two fused carpels. It is more or less flattened, grooved, and densely covered with uniseriate hairs (white in the living state; Rizzini & Occhioni, 1949). The septum is oriented perpendicular to the widest part of the ovary, parallel to the outer sepal whorl (wrongly illustrated by Rizzini

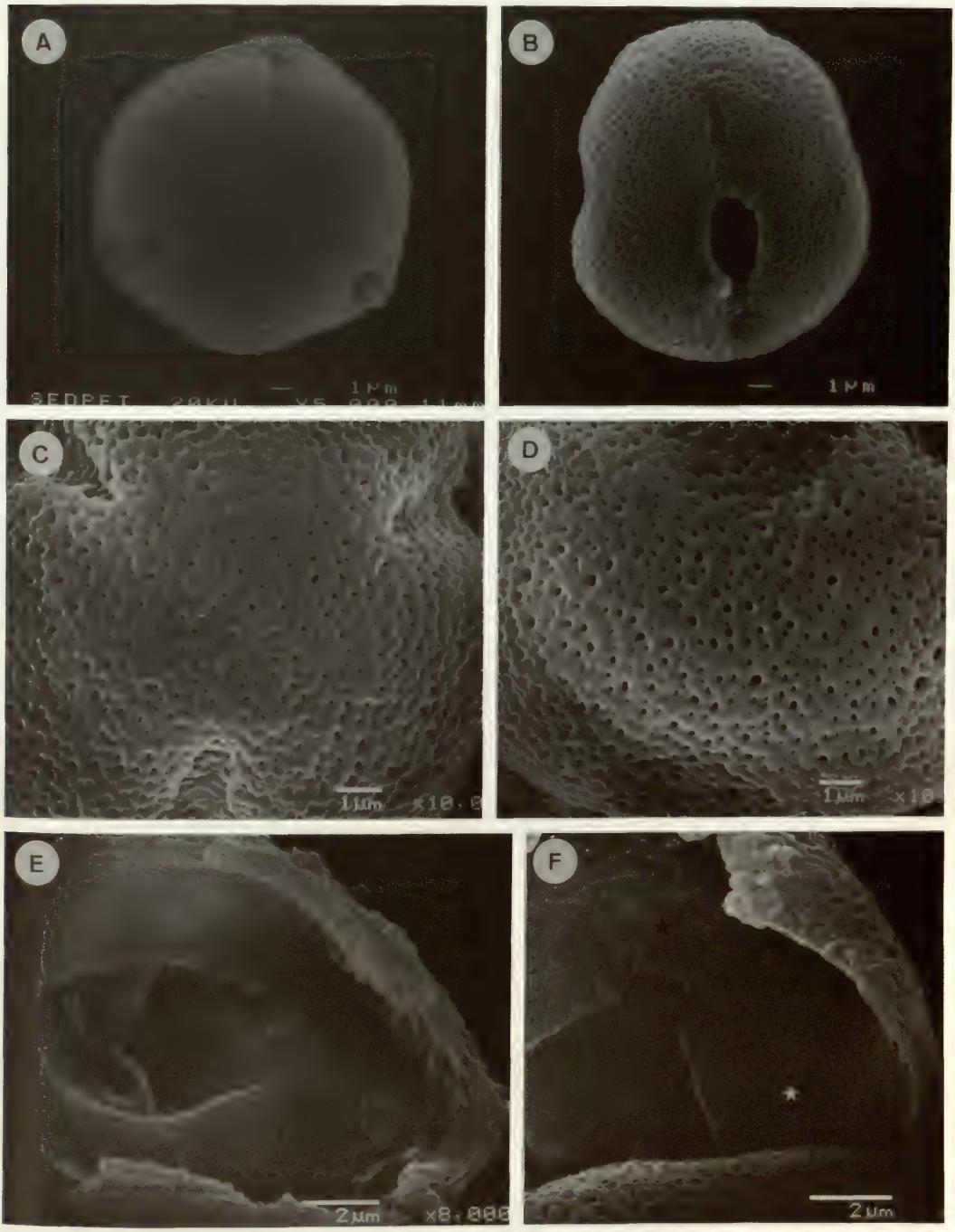


Figure 13. Pollen morphology of *Dialypetalanthus fuscescens* (SEM). A–D. Entire pollen. E, F. Broken pollen.—A. Polar view with well-developed apocolpium.—B. Equatorial view of ecto- and mesoaperture.—C. Detail of the apocolpium.—D. Detail of the mesocolpium.—E. Endocolpus.—F. Endexine ornamentation; note the difference between the warty (white star) and weaker looking zone at the top of the endocolpus (black star). After *de Albuquerque et al. 1295.*

& Occhioni, 1949). In very young buds, the two halves of the septum[4] are fused in the lower part of the ovary. In the upper part, however, they are distinct (Fig. 12A). In mature flowers, the septum is continuous throughout the ovary (Fig. 12B). As a consequence of this septal development, the placenta is U-shaped. This can be seen mainly in young flowers, where septal development is still incomplete, but even in mature fruits the apical split of the placenta is often clearly visible (Fig. 12E). Placentation is therefore axile in the lower part of the ovary and parietal in the upper part. This is often obscured by the fact that the ovules and seeds are closely packed together. Anatomically, the placenta is characterized by the occurrence of cells that are filled with crystal sand (Fig. 12B). Each locule contains numerous ascending, imbricate ovules. Even before anthesis they have the sigmoid shape that is characteristic of the seeds. Most authors (Kuhlmann, 1925; Rizzini & Occhioni, 1949; Cronquist, 1981) have described the ovules as bitegmic. However, we believe that the exotestal seed-coat structure (described later) indicates that the ovules are in fact unitegmic, as was already mentioned by Dahlgren and Thorne (1984). The style is long (up to 12 mm) and glabrous. The papillose stigma is shortly bilobed (Fig. 12C). In stained sections, the papillae are very dark, indicating that the stigma probably secretes a sticky substance in vivo. In bud stage the style is tightly enclosed by the stamens. After anthesis it elongates and rises above the androecium. The style persists even after the other floral parts (with the exception of the calyx lobes) have fallen off. In mature fruits, it falls off as well. The epidermal cells of the style are somewhat smaller than the cortical cells. The latter are more or less arranged in radial rows. The center of the cortex is formed by the transmission tissue. On each side of the transmission tissue there is a small vascular bundle. Cells containing crystal sand occur scattered through the style. Very occasionally, prismatic crystals occur as well. At the base of the style, on top of the ovary, there is a low annular disk, covered with long unicellular trichomes (Fig. 12D). Based on its position (inside the androecial whorls), the origin of the disk is most probably gynoecial and not receptacular. The nature of the secretion, if any, is not known. Just as the style, the disk is characterized by the presence of cells containing crystal sand. The ovary wall shows few striking characters. In the subepidermal zone, numerous tannin idioblasts occur. A clear zone of flattened cells forms the wall of the locules. This zone transforms into a sclerified endocarp in the fruit stage.

Fruit and seeds. *Dialypetalanthus* bears fruits starting from the end of March or beginning of April (immature fruits are green). The fruit (Figs. 14, 15) is an elongated to more or less round (1.2–1.8 × 0.5–0.9 cm), bilocular capsule with persistent calyx lobes. In old capsules these calyx lobes may break off. The bracts and bracteoles are deciduous. The top of the fruit often protrudes above the calyx lobes. The hairy disk as well as the scars of the other floral structures remain visible (Fig. 15A). The fruit is sparsely covered with hairs (more densely so at the base of the calyx lobes), becoming almost completely glabrous when the fruit grows older. After maturation, the fruit splits at first along the septum (from the top downward), by which the outer calyx lobes are split in two. Afterward the locules are split (equally from the top downward) and the seeds set free (Fig. 15A, B). The four parts of the fruit wall remain attached together at the base.

Anatomically, the fruit consists of a thin exocarp, a "fleshy," fibrous mesocarp (due to the vascular bundles that are situated here), and a strongly sclerified endocarp. The exocarp and mesocarp can be easily removed, leaving two coffee-bean-like halves (i.e., endocarp and seeds). When a locule is opened, the numerous seeds and well-developed, U-shaped placenta are visible (Fig. 15B).

The seeds are rather small (up to 7 mm long, but usually smaller and about 1 mm wide at the widest part). Their sigmoid shape (Fig. 16A) causes a rotation when they fall out of the fruit and probably allows further dispersal by wind. The seeds have a wing that is well developed basally and apically, and extremely narrow in the central endosperm-bearing part (Fig. 16E). They are attached to the placenta with the basal part of the wing. The apical part of the wing differs from the basal in that it is wider and not twisted. The endosperm and embryo, visible as a distinct swelling in the center of the seed, are present in only a minority of the seeds. The majority of the seeds are devoid of embryos; some of the examined fruiting specimens seemed to lack embryos almost completely. The seeds are exotestal (sensu Corner, 1976). The endotesta consists of a few layers of crushed cells. Only in the wings is a clear cellular structure visible (Fig. 16D). The inner tangential walls of the exotestal cells have a reticulate thickening pattern (lumina mostly about 10 μm, wider than the muri and often in two rows); their radial walls are also thickened

[4] Each septal half is formed by fusion and subsequent inward growth of the two carpels; finally, the septal halves meet in the center of the ovary.

Figure 14. Fruiting specimen of *Dialypetalanthus fuscescens* (*Silva & Morio 3238*, NY); bar = 5 cm.

(Fig. 16B, C). The seeds have a thin but very obvious, oil-containing endosperm (Fig. 16E). The embryo is large, straight, and has two short cotyledons; in cross section it is round.

Pollination Biology

Rizzini and Occhioni (1949) are the only authors who postulated a pollination strategy for *Dialypetalanthus*. They claimed that *Dialypetalanthus* shows "obvious adaptations for anemogamy," namely many light, dry and small pollen grains. However, Juncosa and Tomlinson (1987: 1315) pointed out that "the existence of light powdery pollen in the taxa with animal pollination is an example of the way in which pollen characteristics may be misleading about the method of pollination." In our opinion, Rizzini and Occhioni's (1949) hypothesis is wrong. The pollen characteristics mentioned as well as the exposed stamens and stigma of *Dialypetalanthus* are indeed often found in wind-pollinated taxa, but the following facts are hardly brought in line with anemogamy: bisexual flowers, unexposed inflorescences, a large attractive corolla (although it falls off soon after anthesis), fragrant flowers (described by Rizzini and Occhioni as "jasmine"), a disk that may secrete nectar (or oil), locular appendages that may have a reward function for pollinators, numerous ovules (indicating the need of successful pollination, contrary to wind-pollinated species, which mostly have few ovules

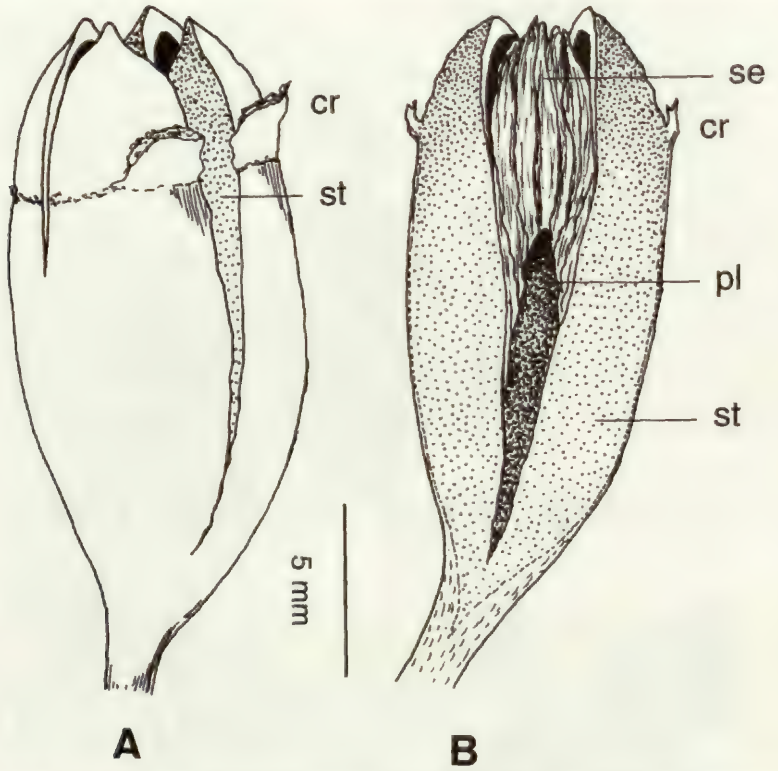


Figure 15. Fruit structure of *Dialypetalanthus fuscescens*.—A. Fruit in late stage of opening, showing deep septicidal and more shallow loculicidal slits.—B. Septal view of a half fruit in the same stage after artificial separation; cr = calyx remnants and scars, st = septum, se = seeds, pl = placenta. After *Silva & Morio 3238* (A) and *Silva 740* (B).

per style) and pollen sacs closely associated with the filament instead of the versatile anthers that are typical of wind-pollinated species. Moreover, one should bear in mind that *Dialypetalanthus* is a rainforest tree. The dense vegetation of mostly evergreen species in rainforests, the large amount of precipitation, and the low turbulence due to the closed canopy, by which pollen cannot stay in the air long enough to cause successful pollination, make wind pollination unlikely. All of these morphological and ecological data strongly suggest animal pollination. A plausible type of pollination is cantharophily. Beetles are especially attracted to white, fragrant flowers with abundant and easily attainable pollen (Willemstein, 1987). All of this is offered by *Dialypetalanthus*. Grant (1950) stated that an inferior ovary may be an adaptation to destructive pollinators (in this case beetles) as a protection for the vulnerable ovules. Cantharophily would be a good explanation for the simultaneous occurrence of numerous stamens and an inferior ovary in *Dialypetalanthus*. The rough flower treatment that is so typical for beetles would also explain the earlier-mentioned lignified zones in the stamens and the overall firm, fleshy structure of the flower.

On the other hand, pollination by bees seems to be an acceptable alternative, because the poricidal anthers may point to buzz-pollination. Moreover, D'Arcy et al. (1996) stated that the occurrence of oxalate packages is rather typical for bee-pollinated species. The pollen becomes mixed with the calcium oxalate crystals when the anthers are vibrated by the insect, although it is still unclear what the crystals are used for. Field observations are needed to establish the pollination strategy of *Dialypetalanthus*.

Distribution and Ecology

In the past it was assumed that *Dialypetalanthus* occurs mainly in the eastern part of Brazil, around Belém (Robbrecht, 1994; Nicholas & Baijnath, 1994). This was probably due to the fact that the first collections (*Kuhlmann 1514*; *Ducke 17921*, *23660*, and *21684*) were from this region. The specimens presently available reveal, however, that the center of distribution is in the northern border

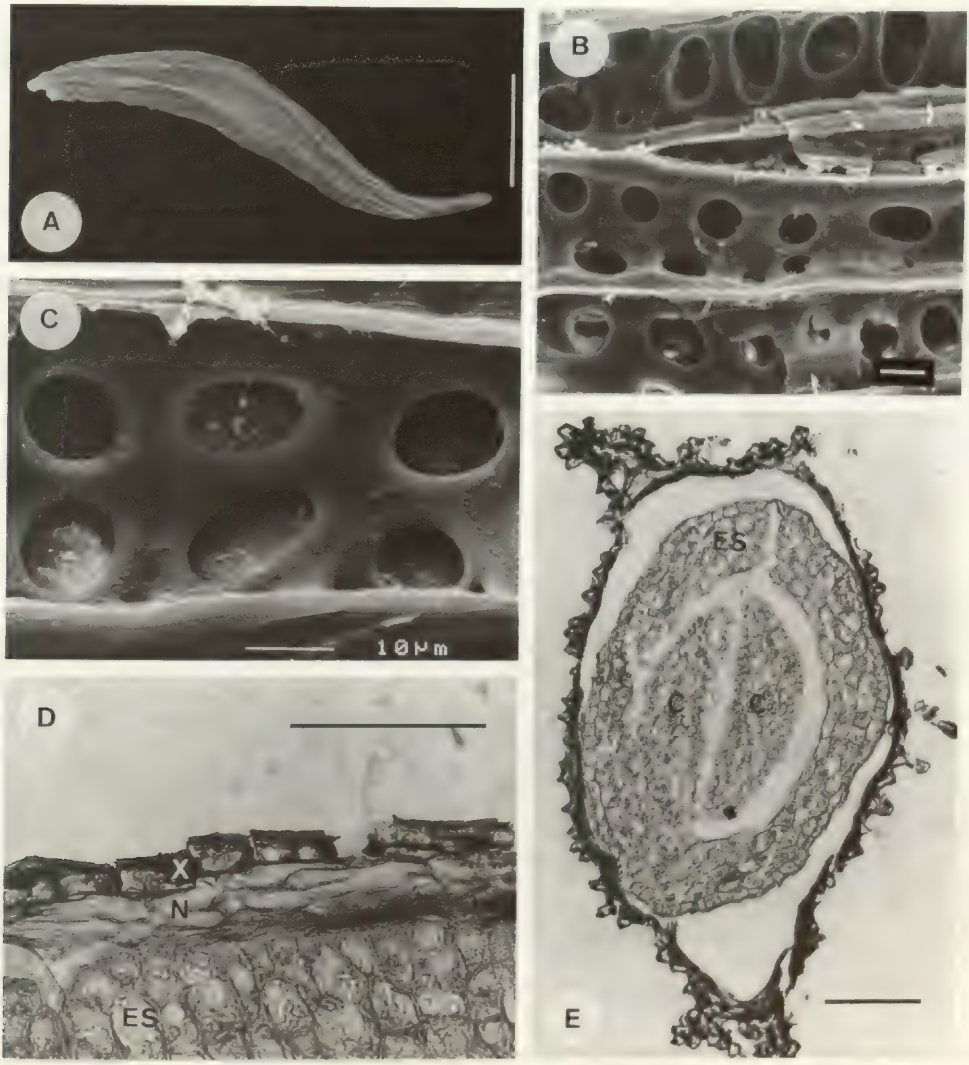


Figure 16. Seed morphology and anatomy of *Dialypetalanthus fuscescens*. (A–C SEM; D, E LM.)—A. Entire seed with typical sigmoid shape (base of seed is at the right); bar = 1 mm.—B. Pitted thickened inner tangential walls of the exotestal cells; bar = 10µm.—C. Detail of the thickening pattern shown in B.—D. Tangential section of the seed coat showing the thickened exotestal cells (X), crushed endotestal cells (N), and endosperm (ES); bar = 0.1 mm.—E. Transverse section of seed; note the cotyledons (C) and well-developed endosperm (ES); bar = 0.1 mm. After *Thomas et al. 5205* (A, D, E) and *Silva 740* (B, C).

region between Bolivia and Brazil (Guajará-Mirim, Costa Marques, Pôrto Velho, Rondônia, Rio Branco) (Fig. 17). The distribution area of *Dialypetalanthus* is situated in Takhtajan's (1986) Amazonian Province, i.e., the southern half of his Amazonian region. In the phytogeographic division of Andersson (1992), *Dialypetalanthus* occurs in the (i) western Amazon of Colombia, Peru, and Brazil; (ii) central Amazon of Brazil; and (iii) eastern Amazon of Brazil.

Although the tree inhabits the terra firme forest (information derived from herbarium labels), it seems to be linked to the rivers in one way or another. This could of course be due to the fact that rivers are avenues for collectors to reach the collecting localities. *Dialypetalanthus* mostly grows on sandy or gravelly soils, schist outcrops (where it occurs together with such taxa as *Orbignya phalerata* Mart., *Hevea*, and *Bertholletia*), or granite outcrops. *Dialypetalanthus* has been found only south of the Amazon River. No collections are known from the region between the Amazon and the Orinoco.

According to Prance (pers. comm.), *Dialypetalanthus* is a rather common tree in Brazil, occurring

Figure 17. Distribution map of *Dialypetalanthus fuscescens.*

in primary forest as well as in partly disturbed, more open regions. However, as the forest becomes more and more devastated due to agricultural expansion and the construction of dams, it is not impossible that *D. fuscescens* will become a threatened species in the near future.

Specimens examined (square brackets indicate coordinates determined by means of place descriptions). BOLIVIA. **Beni:** Road Guajará-Mirim-Cachuela Esperanza, Rio Yata, [11°S, 66°W], *Anderson 11865* (NY). **Pando:** Nicolás Suárez, between Cobija and Porvenir, [11°S, 68°30′W], *Fernández Casas & Susanna 8188* (NY); Puerto Oro, 74 km SW of Cobija, 11°25′S, 69°05′W, *Pennington et al. 143* (K). BRAZIL. **Acre:** Mun. Sena Madureira, basin of Rio Purus, Rio Macauã, Colocacão Apui, 09°48′S, 69°11′W, *Daly et al. 8068* (NY not seen); Mun. Sena Madureira, basin of Rio Purus, Rio Macauã, Fazenda São José, 09°46′S, 69°09′W, *Daly et al. 8095* (NY not seen); Mun. Rio Branco, road Rio Branco-Pôrto Velho, km 22, Quinoá, [10°S, 67°30′W], *de Albuquerque et al. 1295* (NY, US); Mun. Sena Madureira, Rio Macauã, Seringal Santa Luzia, 09°39′S, 69°01′W, *de Lima et al. 575* (NY not seen). **Amazonas:** Rio Madeira, Humaitá, [07°30′S, 63°W], *Ducke 35428* (K, US). **Goiás:** Xambioa, 06°26′S, 48°27′W, *Edison Mileski 397* (MG not seen); Rio Araguia, região de Araguatins, Ilha Santa Isabel, [06°30′S, 49°W], *Oliveira 1572* (NY). **Maranhão:** Mun. Santa Luzia, Fazenda Agripec da Varig, Rio Pindaré, [04°S, 45°30′W], *Lobo et al. 328* (K, NY, US); Funai, 40 km from Arame, *Vilhena et al. 1003* (NY). **Mato Grosso:** Dardanelos, Sta. Elena, *Cordeiro 175* (NY); Fazenda Cachimbo, [09°30′S, 55°W], *Cordeiro 1085* (NY); Rio Madeira, Salto Theotônio, [15°S, 59°30′W], *Ducke 22816* (K, US); Rio Tapajós, Salto Augusto, *Kuhlmann 1514* (NY) SYNTYPE; Rio Juruena, Aripuanã, Fontanilha, [10°30′S, 58°W], *Silva & Morio 3238* (NY). **Pará:** Rio Tapajós, Itaituba, [04°S, 55°30′W], *Ducke 17921* (K, US) SYNTYPE; Serra de Santarém, [02°30′S, 55°W], *Ducke 21684* (K, NY); Serra de Santarém, [02°30′S, 55°W], *Ducke 23660* (US); Igarapé Fernando do Noronha, Rio São Manuel, Caldeirao, [9°S, 64°30′W], *Pires 3853* (NY, US); Rio Itacaiuna-Rio Tocantins, 05°30′S, 50°15′W, *Pires et al. 12531* (MG not seen); Região Gorotire, Rio Xingu, 06°38′S, 52°00′W, *Silva 740* (NY); Cabeça, 09°45′S, 51°20′W, *Silva 740* (NY); Tucuruí, Breu Branco, [03°45′S, 49°45′W], *Silva 5457* (MG not seen); Rio Tocantins, Tucuruí, Breu Branco, [04°S, 49°W], *Silva & Bahia 3514* (NY); Rio Itacaiuna, 2 km downstream from ferry crossing to AMZA camp3-alfa, 05°53′S, 50°30′W, *Sperling et al. 6167* (NY). **Rio de Janeiro:** Rio de Janeiro, cultivated plant in the Botanical Garden, *Occhioni et al. 57941* (K). **Rondônia:** Mun. de Presidente Medici, BR364, road Cuiaba-PôrtoVelho, km 300, 11°12′S, 61°62′W, *Cid et al. 4801* (NY); Mun. Costa Marques, BR429, near Rio Cautarinho at 5 km of BR, 12°10′S, 63°25′W, *Cid Ferreira 8649* (NY); Mun. Pôrto Velho, Estrada da Serra do Balateiro a 3 km da Vila Campo Novo, 10°35′S, 63°39′W, *Cid Ferreira 8895* (NY); Mun. Alvorada do Oeste, BR429, estrada para Costa Marques, Serra da Onça a 35 km da cidade de Alvorada do Oeste, 11°30′S, 62°30′W, *Cid Ferreira 9018* (NY); Guajará-Mirim, border region with Bolivia, [11°S, 65°W], *Cordeiro 1007* (MG not seen); Pôrto Velho, [10°S, 63°W], *Maciel et al. 1674* (MG not seen); 2 km of Guajará-Mirim, [11°30′S, 65°W], *Nascimento 316* (MG not seen); 15 km N of Ariquemes, on hwy. BR364 and 1 km E on "Linea 75," 09°47′S, 63°05′W, *Nee 34357* (NY, US); 21 km SE of Ariquemes, on hwy. BR364 and 1 km E on "Linea 45," 10°07′S, 62°56′W, *Nee 34426* (NY); Mun. Costa Marques, 2 km W of Rio Cautarinho, along hwy. BR429, 12°04′S, 63°28′W, *Nee 34472* (NY); Mun. Costa Marques, road Costa Marques-Forte Príncipe da Beira, 9.5 km E of Forte Príncipe da Beira, 12°26′S, 64°20′W, *Nee 34518* (NY); road Abuña-Guajará-Mirim, 1 km N of Riberão, [10°30′S, 65°W], *Prance et al. 6526* (NY, US); vicinity of São Lorenco Mines, basin of Rio Madeira, 09°33′S, 65°06′W, *Prance et al. 8967* (NY, US); Rio Urupa, [11°S, 62°W], *Rosa 428* (MG not seen); Pôrto Velho, [08°45′S, 64°W], *Rosa 485* (MG not seen); Mun. de Ariquemes, Mineração Mibrasa, Setor Alto Candeias, km 128, 10°35′S, 63°35′W, *Teixeira et al. 562* (NY); Pôrto Velho, Represa Samuel, 09°04′S, 63°15′W, *Thomas et al. 5205* (NY, US). PERU. **Madre de Dios:** Tambopata, 12°49′S, 69°18′W, *Gentry et al.* 45957 (NY). LOCALITY UNCERTAIN. *Ferreira 438* (K).

Discussion

Because of its polyandrous androecium, most authors (Cronquist, 1968; Dahlgren, 1975; Emberger, 1960; Melchior, 1964; Rizzini & Occhioni, 1949; Stebbins, 1974) have placed *Dialypetalanthus* near the Myrtales (more precisely near the Myrtaceae and Melastomataceae) rather than near the Gentianales. However, a relationship between *Dialypetalanthus* and the Myrtales is unlikely because Myrtales have internal phloem, leaves typically covered with glandular dots, and seldom have paracytic stomata, unlike *Dialypetalanthus.* Moreover, Myrtaceae lack septate fibers and their wood is of-

ten characterized by well-developed axial parenchyma. Melastomataceae have an acrodromous venation pattern, a synapomorphy for this family according to Renner (1993); this venation pattern does not occur in the Dialypetalanthaceae. The only vegetative resemblances between *Dialypetalantus* and Myrtales are the simple, opposite, entire leaves and the vestured intervessel pits of the wood, but these characters are common in the Gentianales as well and are by themselves insufficient to support a close relationship. The stipules of *Dialypetalanthus* give no more indication of relationship. Myrtales are exstipulate (e.g., in Melastomataceae) or possess rudimentary stipules (e.g., Myrtaceae, Trapaceae; Dahlgren & Thorne, 1984). Gentianales s.l. often have well-developed (Rubiaceae, Loganiaceae) or rudimentary stipules (Apocynaceae).

In vegetative (and also fruiting) stage, *Dialypetalanthus* is hard to distinguish from certain Cinchonoideae (Rubiaceae). Robbrecht (1994: 23) noted that "the habitual resemblance of vegetative or fruiting material to Rubiaceae is impressive, and almost all Amazonian field workers assign the tree to the Rubiaceae." Indeed, the simple, opposite, entire leaves and the well-developed stipules are characteristic of Rubiaceae as well as *Dialypetalanthus*. The paracytic stomata, colleters of the standard Rubiaceae-type at the inside of the stipules, the lack of internal phloem, the vestured pits, and septate libriform fibers are shared as well.

The following features are in our opinion critical to assess the relationship of *Dialypetalanthus*, and need to be discussed in detail:

Dendritic hairs. Dendritic hairs have a rather restricted taxonomic distribution in the angiosperms (Theobald et al., 1988). Our observation of the occasional occurrence of dendritic and stellate hairs on the petioles and stamens of *Dialypetalanthus* is new. Rubiaceae generally have simple or uniseriate trichomes (Robbrecht, 1988), although Theobald et al. (1988) mentioned the occurrence of non-glandular stellate hairs in this family (they did not specify species or genera, however). Stellate hairs were not mentioned in Verdcourt's (1958) and Robbrecht's (1988) survey of Rubiaceae trichomes. Since stellate and dendritic hairs each were observed only once in *Dialypetalanthus*, it remains unclear whether any systematic value should be attached to it.

Choripetaly. Dialypetalanthus is characterized by the occurrence of four free petals. According to Hutchinson (1959), the free petals of *Dialypetalanthus* are no reason to exclude it from the Rubiaceae, because "the corolla is divided to the base in at least three genera" (p. 386) [*Molopanthera* (Rondeletieae; Delprete, 1996), *Synaptanthera* (Hedyotideae; note that the correct name is *Synaptantha*; Robbrecht, 1994), and *Aulacodiscus* (= *Pleiocarpidia*; Urophylleae; Robbrecht, 1994)]. However, the three genera cited by Hutchinson are characterized by a deeply to very deeply divided corolla tube instead of free petals. Schumann (1891) described the corolla of *Molopanthera* as "sehr tief geteilt" (p. 54) and that of *Synaptantha* as "fast bis zum Gründe geteilt" (p. 24). Bremekamp (1940a) paid no special attention to the corolla in his monograph of *Pleiocarpidia*. He described it as "breviter hyperocrateriformis, tubo suburceolato." If *Pleiocarpidia* possessed free petals, this most probably would not have escaped Bremekamp's attention.

Hedstromia (Psychotrieae) has also been described as "having five essentially free petals" (Darwin, 1979) or "polypetalous" (Smith & Darwin, 1988), but again we assume that the utmost base of the corolla lobes is fused, as the stamens are said to be "attached at base of the corolla" (Smith & Darwin, 1988). The same authors (p. 239) described *Mastixiodendron* as having "semisuperior ovaries and polypetalous corollas, characteristics that occur in a number of rubiaceous tribes." The latter statement apparently only refers to semisuperior ovaries.

Altogether, *Mastixiodendron* seems to be the only genus in Rubiaceae that may possibly have free petals. Note that this genus has previously been placed in the Cornaceae because of its "choripetaly" (Melchior, 1925, fide Darwin, 1977). However, the only modern documentation of *Mastixiodendron* (Darwin, 1977) contains insufficient information to judge its choripetaly. It states that "at anthesis, the corolla lobes are always entirely free," but gives no information on early ontogenetic stages or the state of immature corollas. We have looked at flowers of *Mastixiodendron* (*M. pachyclados* (Schum.) Melch., *Schodde & Craven 4245*, L) in order to verify the true nature of the corolla. At anthesis, the corolla lobes are indeed entirely free. In bud stage, however, they are fused; when the flower opens they split down to the base along the fusion margins. The mature stamens are completely free from the corolla (and alternating with the lobes) and are inserted below the intrastaminal disk. Thus, all reports of true choripetaly within the Rubiaceae seem to be based on inadequate observations.

Free petals are, however, not the major problem in postulating a relationship between Rubiaceae and *Dialypetalanthus*, since both taxa could have

developed from a common ancestor with free petals. In this context, it is interesting to recall that the Gentianales are included in the Cornidae in some modern angiosperm classifications (Frohne & Jensen, 1992; Smets, 1988 unpublished Ph.D. thesis). Here, the basal family Cornaceae (Cornales) does have free petals. Whereas Lee and Fairbrothers (1978) demonstrated serological links between Rubiaceae (a derived family of the Cornidae) and Cornaceae, *Dialypetalanthus* seems to add a morphological dimension to this connection.

Polyandry. The major problem in postulating a close relationship between *Dialypetalanthus* and Rubiaceae, and at the same time the strongest argument of Rizzini and Occhioni (1949) for the inclusion of *Dialypetalanthus* in Myrtales, is the polyandrous androecium. Rizzini and Occhioni stressed the fact that Rubiaceae are isomerous: "Ora, sabemos serem as Rubiaceae notáveis pela fixidêz de seu número estaminal: este é sempro igual ao de segmentos da corolla, a tal ponto de, mesmo em formas anômalas por cultivo, persistir essa característica" (p. 249). As an extreme example, they mentioned *Gardenia thunbergii* L.f., which sometimes has up to 11 petals and 11 corresponding stamens. Note that pleiomery is a rather common feature within the Rubiaceae–Gardenieae, and that it is not restricted to cultivated species (Robbrecht & Puff, 1986).

Polyandrous androecia are, according to Hutchinson (1959), also known in the genus *Praravinia* (Rubiaceae–Urophylleae). Bremekamp (1940b) attributed the notion of polyandry in *Praravinia* to Korthals's protologue of the genus, but doubted its correctness, because all the specimens he examined were isomerous.

Whereas the polyandry of *Praravinia* is probably based upon wrong observations, this cannot be said of *Coprosma* (Anthospermeae); some species have a secondarily increased stamen number [e.g., *C. nephelephila* Florence, corolla 5–6-merous, stamens 5–8(–12); Florence, 1986]. *Theligonum*, now generally accepted as being a rubiaceous genus (Robbrecht, 1994; Rutishauser et al., 1997), is polyandrous as well. In *Coprosma* and *Theligonum*, polyandry seems to be an adaptation to anemophily.

Oxalate packages. Our study revealed the occurrence of oxalate packages (O.P.'s) in the anthers of *Dialypetalanthus* at a moment when these peculiar structures were receiving renewed attention (D'Arcy et al., 1996). According to D'Arcy et al., the only positive reports of O.P.'s are from the Solanaceae, Ericaceae, Theophrastaceae, Balsaminaceae, Bromeliaceae, Araceae, Lemnaceae, Arecaceae, Liliaceae, Onagraceae, and Tiliaceae. In the Dialypetalanthaceae, the O.P.'s are different from the common or Solanaceae type described by these authors, since they are not located in the stomium but in apical, sterile appendages of the anthers.

O.P.'s are not recorded from the candidate relatives Myrtaceae, Melastomataceae, or Rubiaceae. We have observed, however, very obvious O.P.'s in *Cinchona pubescens* M. Vahl. (unpublished); here they occur as crystal sand and belong to the type described in Solanaceae (D'Arcy et al., 1996), i.e., situated at the stomium and running the length of the anther. Since the Rubiaceae are characterized by the common occurrence of several types of calcium oxalate crystals, one may expect that O.P.'s occur much more generally in this family but remain overlooked.

Rubiaceae and Dialypetalanthaceae both have O.P.'s, but these belong to a different morphological type. It seems that the taxonomic distribution of these anther structures is insufficiently known at present to draw further systematic conclusions.

Dimery. The calyx and corolla of *Dialypetalanthus* are initiated as dimerous whorls. Dimery has a rather restricted occurrence within the dicotyledons. As far as we know, it is only reported for the Begoniaceae, Berberidaceae, Cecropiaceae, Brassicaceae, Capparidaceae, Ebenaceae, Elatinaceae, Fumariaceae, Gunneraceae, Lauraceae, Nepenthaceae, Nymphaeaceae, Oleaceae, Onagraceae, Phytolaccaceae, Polygonaceae, Portulacaceae (Ronse Decraene & Smets, 1991: 95), Ranunculaceae, and Winteraceae (Watson & Dallwitz, 1991; Ronse-Decraene, 1992 unpublished Ph.D. thesis). Almost all Myrtales and Gentianales having four sepals and petals are truly tetramerous instead of dimerous, as can be derived from their floral diagram. Therefore, the dimery of *Dialypetalanthus* more or less isolates the genus. It should be noted, however, that *Theligonum* (Rubiaceae) may be dimerous as well (Rutishauser et al., 1997).

Anther dehiscence and monadelphy. Rizzini and Occhioni (1949) considered the united filaments and porate dehiscence of the anthers as strong arguments to exclude *Dialypetalanthus* from the Rubiaceae. However, porate anthers occur in the rubiaceous genera *Rustia* (apically porate; Delprete, 1995), *Tresanthera* (laterally porate; Delprete, pers. comm.), and *Argostemma* (Robbrecht, 1988). The character is definitely without value to corroborate or exclude a possible rubiaceous relationship.

Monadelphy is not especially rare in Rubiaceae. It occurs, for example, in *Capirona, Bikkia, Coutarea,* and *Exostema* (Robbrecht, 1988) and is even

considered to be a synapomorphy of the Chiococceae (Bremer & Struwe, 1992). In all these cases, however, the ring formed by the filament bases is attached to the corolla tube. In this feature Rubiaceae differ from *Dialypetalanthus*. However, in a few genera of the Chiococceae sensu Delprete the stamens are not attached to the corolla tube, but on top of the ovary (Delprete, pers. comm.).

Gynoecial structure. Whereas the corolla and androecium of *Dialypetalanthus* and Rubiaceae show fundamental differences, their gynoecial structure is completely similar. Both *Dialypetalanthus* and many Rubiaceae are characterized by an inferior, bilocular gynoecium with numerous ovules in each locule and a disk on top of the ovary, surrounding the base of the style. The supposedly primitive (Leinfellner, 1951), U-shaped placentas of *Dialypetalanthus* occur in numerous genera of the Rubiaceae as well (De Block & Robbrecht, 1997).

The numerous, ascending, imbricate ovules of *Dialypetalanthus* offer a strong argument for exclusion of this genus from the Myrtales. As Dahlgren and Thorne (1984) already concluded from observations of the seed-coat structure, these ovules are unitegmic. This character is typical for Gentianales and Cornales, but is lacking in Myrtales (except for *Syzygium*; Dahlgren & Thorne, 1984).

With the exception of Melastomataceae and Memecylaceae, both Myrtales and Gentianales are provided with a more or less well-developed disk. Smets (1988) stated, however, that these disks may not be homologous, because the disk of Myrtales has a receptacular origin, whereas that of Gentianales is gynoecial. The disk of *Dialypetalanthus* arises late in the floral ontogeny as a swelling, situated at the inside of the androecial ring, surrounding the base of the style. Its origin is therefore most probably gynoecial, as in Gentianales.

Pollen. Erdtman (1971) considered the pollen of *Dialypetalanthus* to be more similar to pollen of Rhizophoraceae than to that of Myrtaceae, Melastomataceae, and Rubiaceae. We do not deny the resemblances between the pollen of *Dialypetalanthus* and certain Rhizophoraceae, nor the differences from that of Myrtaceae (often synaperturate pollen) and Melastomataceae (usually with pseudocolpi); however, the pollen fits perfectly within the pollen morphological variation of the Rubiaceae. At the time Erdtman wrote his book, this variation was insufficiently known, as is demonstrated by his limited treatment (only ± 5 % of the genera) of this huge family. The tricolporate, tectate-perforate pollen of *Dialypetalanthus* is now known to be the most common type encountered in Rubiaceae (Robbrecht, 1988).

Fruit and seeds. The capsules with numerous winged seeds of *Dialypetalanthus* are hardly distinguishable from those of certain Rubiaceae–Cinchonoideae. For example, capsules that split into four parts and seeds with basally attached seed wings (as in *Dialypetalanthus*) are very common in several genera of the Rondeletieae s.l. (Delprete, 1996). Winged seeds occur in many Rubiaceae tribes. Seed wings are extremely diverse; the condition found in *Dialypetalanthus* (wing mainly restricted to base and apex) occurs, e.g., in *Mitragyna* (Coptosapelteae; Stoffelen et al., 1996: fig. 2I). Although Rizzini and Occhioni (1949) thought that winged seeds are not very useful for classification purposes, they add another resemblance between the fruit and the seeds of *Dialypetalanthus* and the Cinchonoideae.

The seed-coat structure of *Dialypetalanthus* cannot be classified as one of the three seed-coat types that Corner (1976) distinguished for the Myrtales, and therefore presents another argument for excluding *Dialypetalanthus* from this order. On the contrary, the pitted thickenings of the inner tangential walls of the exotestal cells and the crushed endotestal cells of the seed coat of *Dialypetalanthus* are considered to be typical of the Cinchonoideae (Bremekamp, 1966; Robbrecht, 1988).

Myrtales (with the exception of some rare cases in Myrtaceae, where scanty endosperm may be formed) are characterized by the lack of endosperm (Dahlgren, 1991). This again argues against inclusion of *Dialypetalanthus* in the Myrtales. With its well-developed endosperm, it fits far better in the Gentianales (and Rubiaceae).

Conclusion

Summarizing the evidence obtained from floral and fruit structure, a close relationship between *Dialypetalanthus* and Myrtales is unlikely because of the following character states of *Dialypetalanthus*: unitegmic ovules, gynoecial disk covered by unicellular trichomes, exotestal seed coat, and well-developed endosperm. Gynoecial structure, fruit, and seeds show remarkable resemblances with the Rubiaceae (more specifically the subfamily Cinchonoideae), whereas pollen morphology does not exclude a relationship with that family. The dimerous origin of calyx and corolla, the free corolla lobes, and the supposed cantharophily are unique, possibly primitive, features of *Dialypetalanthus*, giving it a somewhat isolated position. The interpretation of the polyandrous androecium remains

problematic as long as its origin is not elucidated by ontogenetic studies. We consider *Dialypetalanthus* to be a textbook case of heterobathmy, combining primitive features (the presence of stipules and U-shaped placentas may be added to the characters enumerated above) with derived gynoecial features. Our observations consequently corroborate a *Dialypetalanthus*–Rubiaceae relationship, but the genus can clearly not be included in that family. The translation of this conclusion into a proposal for a classification above the family level (i.e., should the Dialypetalanthaceae be placed in the order Gentianales s.l. or in the Rubiales) is not easy. Since the delimitation of the Gentianales, and more specifically the position of the Rubiaceae, is still problematic and subject to frequent change (Nicholas & Baijnath, 1994; De Laet & Smets, 1996), it seems best to maintain at present a widely conceived order Gentianales, including the Dialypetalanthaceae and Rubiaceae and arising from a cornalean stock. In order to gain a better understanding of the position of the Dialypetalanthaceae within this gentianalean complex (e.g., should Dialypetalanthaceae and Rubiaceae be put together in the Rubiales s.l., closely related to the Gentianales s. str.?), a cladistic analysis including Gentianales, Cornales, and other members of the Cornidae alliance most certainly would be very useful. In the latter context, however, it is regrettable that phytochemical (Darnley-Gibbs, 1974; Hegnauer, 1990), floral ontogenetic, and macromolecular data of *Dialypetalanthus* are still very poorly or not at all known. Consequently, future research should mainly concentrate on these and other missing characters of *Dialypetalanthus* to further elucidate its systematic position.

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CONSPECTUS OF THE GENUS *PALICOUREA* (RUBIACEAE: PSYCHOTRIEAE) WITH THE DESCRIPTION OF SOME NEW SPECIES FROM ECUADOR AND COLOMBIA[1]

Charlotte M. Taylor[2]

Abstract

Palicourea Aublet comprises about 200 species of shrubs and small trees found throughout the moist and wet Neotropics. This genus is distinguished by characters of the corolla that apparently represent adaptations for pollination by hummingbirds and seems to be a member of a hummingbird-pollinated group closely related to *Psychotria* subg. *Heteropsychotria,* which is generally insect-pollinated. An infrageneric classification is proposed here for 188 species, based largely on characters of the stipules and fruits. This classification comprises two subgenera, one generally lowland, centered in Amazonia, and comprising 52 species in four sections, and the other generally middle to high elevation, centered in the northern Andes, and comprising 136 species in five sections. Several distinctive features shared by species that belong to different sections and in some cases different subgenera are noted. These patterns suggest that at least some features have been derived repeatedly in parallel within the genus. The relatively large number of species of *Palicourea* found at middle and high elevations may be due to the exploitation by this group of hummingbird pollination, together with habitat diversity, distyly, and variation among local populations leading to their reproductive isolation. The following new combinations are made: *Palicourea* sect. *Corymbiferae* (Müll. Arg.) C. M. Taylor, *Palicourea subtomentosa* (Ruiz. & Pav.) C. M. Taylor and *P.* subser. *Subcymosae* (Müll. Arg.) C. M. Taylor; the following new taxa are described: *P.* subg. *Montanae, P.* sect. *Cephaeloides, P.* sect. *Grandiflorae, P.* sect. *Montanae, P.* sect. *Obovoideae, P.* sect. *Pseudoamethystinae,* and *P.* sect. *Psychotrioides*; and the following new taxa are described, illustrated, and classified: *P. anderssoniana, P. anianguana, P. asplundii, P. azurea, P. canarina, P. candida, P. chignul, P. condorica, P. corniculata, P. cornigera, P. deviae, P. gentryi, P. harlingii, P. jaramilloi, P. lugoana, P. luteonivea, P. prodiga, P. subalatoides, P. subtomentosa* subsp. *lojana, P. ulloana,* and *P. vulcanalis.*

Palicourea Aublet comprises about 200 species of shrubs and small trees distributed from central Mexico and the Antilles to southern Peru, Bolivia, Paraguay, and northern Argentina (Fig. 1). This genus has not been surveyed as a whole since Schumann's (1891) review of the family and has never been studied in any detail in its entirety, although several recent regional treatments are available (Steyermark, 1972, 1974; Bacigalupo, 1952; Taylor, 1989, 1993), and monographic work is currently in progress. *Palicourea* is notable for the large number of apparently closely related species it includes overall, and also for the frequent sympatric occurrence of several (to numerous) different species at a given site (e.g., Kappelle & Zamora, 1995; Sobrevila et al., 1983; pers. obs.).

Species of *Palicourea* are typically members of the understory and subcanopy of moist to wet forest, and are found from low elevations to the upper limits of wet montane forest. A few species grow in savanna habitats and show pyrrhophytic adaptations. Both widespread weedy species and locally endemic, apparently more specialized species are found in this genus. *Palicourea* flowers have corollas with relatively well-developed tubes and typically are odorless, brightly colored, and pollinated by hummingbirds; the carnose, usually blue to purple fruits are dispersed by birds. Nearly all *Pali-*

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[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

courea species are distylous; this appears to be the ancestral condition for the genus (Taylor, 1993).

Palicourea is closely related to the neotropical subgenus *Heteropsychotria* Steyerm. of *Psychotria* L. (Taylor, 1996). These groups are separated only by characters of the corolla, as discussed below.

Schumann (1891) presented an infrageneric classification for *Palicourea* as a whole, based primarily on the regional treatments by Mueller (1881, who included it in *Psychotria*) and Grisebach (1861); no subsequent author has made reference to this classification, including Steyermark (1972, 1974), even though he treated 56 and 47 species, respectively, and presented a detailed infrageneric classification for the closely related genus *Psychotria*. No infrageneric classification has been proposed more recently for this genus.

In this article I outline the circumscription of *Palicourea*, present an infrageneric classification, discuss some of the character patterns now evident within the genus, and describe several new taxa.

Circumscription of *Palicourea*

Schumann (1891) was one of the first authors to distinguish *Palicourea* explicitly from *Psychotria*. In his key to genera, he separated *Palicourea* by its bent corolla that is gibbous at the base. He nevertheless included in *Palicourea* species such as *Psychotria domingensis* Jacq. (Schumann, 1891: 115), with white corollas that are curved in the tube but never gibbous at the base (Taylor, 1987), and excluded from it species such as *Palicourea aurantiaca* Miq. (Schumann, 1891: 114), a name here considered synonymous with *Palicourea fastigiata* Kunth and based on a set of specimens with the corollas bright orange, gibbous, and straight to slightly bent at the base, but generally straight in the tube. Thus, his actual circumscription of the genus was not entirely consistent.

Standley (1936, 1938) distinguished *Palicourea* by its "corolla tube elongate, more or less curved, gibbous at the base; branches of the inflorescence usually pale or red or yellow," and this concept was followed closely by Dwyer (1980). Standley placed in *Palicourea* several species with these distinguishing features but with green inflorescence branches and white or nearly white corollas, e.g., *Palicourea andrei* Standl., *P. andaluciana* Standl., and *P. garciae* Standl.; simultaneously he placed in *Psychotria* several similar species that have white or yellow corollas that are swollen at the base and green to brightly colored inflorescence branches, e.g., *Psychotria bella* Standl. [= *Palicourea bella* (Standley) Dwyer], *Psychotria copeyana* Standl. & L. O. Williams [= *Palicourea* garciae], and *Psychotria brenesii* Standl. [= *Palicourea standleyana* C. M. Taylor]. Standley's circumscription of *Palicourea* seems to have been based on the aggregate classification of individual species rather than characterization of the genus as a whole.

Steyermark's (1972, 1974) generic concept of *Palicourea* was more consistent and based more strongly on corolla features. He distinguished *Palicourea* from *Psychotria* in his key as follows (Steyermark, 1974, my translation from the Spanish): "[b]ase of the corolla tube with a slight swelling or a curvature on one side; interior of the corolla tube with a ring of trichomes usually near the base; corolla usually blue, purple, yellow, orange, red, or combinations of these colors; rachis and axes of the inflorescence with similar colors." In practice, species included by Steyermark in *Palicourea* usually also have a relatively well-developed corolla tube.

As a basis for distinguishing *Palicourea* species, I (Taylor, 1989, 1993, 1996) have used corollas with a swollen base closed internally by a ring of pubescence (as emphasized by Steyermark), and the general tendency to have brightly colored floral displays and relatively well-developed corolla tubes. These features appear to represent adaptation for pollination by hummingbirds: nectar accumulates in the enlarged basal part of the corolla and is protected by the ring of pubescence from weaker or smaller flower visitors, and the pollinators are often attracted by the colorful inflorescence displays.

Palicourea appears in general to represent a lineage closely related to or perhaps even derived from *Psychotria* subg. *Heteropsychotria* through adaptation for hummingbird pollination (Taylor, 1989, 1996). This genus has so far been assumed to comprise a monophyletic group (Taylor, 1989, 1996) that can be recognized by the characteristic corolla morphology. Additionally, the pollen of the very few species of *Palicourea* that have been studied lacks or nearly lacks exine (Erdtman, 1952; Taylor, 1996). No evidence has been found to date to suggest that this genus is polyphyletic, although its unusual corolla morphology could conceivably have been derived more than once. A few species that show this characteristic corolla morphology and are similar to other *Palicourea* species, but do not appear to be solely hummingbird pollinated, may represent secondary pollinator shifts. For example, *Palicourea andrei* is very similar to *P. boyacana* Standl., which has tubular orange flowers, but *P. andrei* has sweetly fragrant, tubular white corollas that could also be adapted for insect pollination. As discussed below, hummingbird pollination ap-

Figure 1. Approximate number of species of *Palicourea* by country, for the entire range of the genus. Numbers followed by "+" represent conservative estimates for country floras not yet surveyed in detail.

pears to be an important factor in the diversification of this genus. Adaptations for hummingbird pollination are generally considered to include brightly colored flowers, but these birds frequently do visit, and even actively defend, *Palicourea* plants with green inflorescences and relatively short white corollas (e.g., *P. calophlebia* Standl., Colombia, pers. obs.).

Phytogeography and Ecology of *Palicourea*

Species of *Palicourea* are concentrated in tropical South America; they are also well represented in Central America, particularly in montane Costa Rica and Panama (Fig. 1). Eight species are found in the Antilles, most of them in the Greater Antilles, and more than 32 species are now known from Central America (Taylor, 1989, 1990). In South America, *Palicourea* is widespread in low-elevation wet tropical forests and also shows notable centers of species diversity in wet tropical montane areas.

Palicourea is more species-rich in montane than lowland habitats. When montane species are defined as those predominantly distributed at or above 1000 m elevation (Gentry, 1988), 22 of the 26 species known from Costa Rica can be considered montane (Burger & Taylor, 1993), as can ca. 50 of the ca. 80 species known from Ecuador (Taylor, in prep.). The two subgenera recognized below approximate this habitat distribution: of the 188 species of *Palicourea* classified below, 52 are placed in subgenus *Palicourea*, which is primarily distributed at low elevations, while 136 are placed in subgenus *Montanae*, which is primarily montane. *Palicourea* is usually well represented locally in montane forests in both number of individuals and number of species (e.g., Kappelle & Zamora, 1995; Silverstone-Sopkin & Ramos-Pérez, 1995). The dis-

tributions of most species of subgenus *Montanae* correspond to Takhtajan's (1986) regions, and in particular support his circumscription of the Central American region, which extends south along coastal Colombia into Ecuador, rather than Gentry's (1982) circumscription of this region, which ends in northwestern Colombia. Several groups of apparently closely related species of *Palicourea* are restricted to individual phytogeographic provinces (sensu Takhtajan, 1986).

The relatively greater species diversity of *Palicourea* in montane habitats is very likely due in part to the larger number of different habitats, or microhabitats, in montane regions. In general, low-elevation species of *Palicourea* usually have wider geographic distributions than do montane species, and fewer of the low-elevation species are local endemics. For example, none of the four lowland species known from Costa Rica is endemic and all extend at least as far south as Peru; in contrast, 6 of the 22 montane species from that country are endemic to it and the rest are otherwise found only in Panama or in a few cases in western Colombia. Montane areas have been considered by a number of authors to comprise a greater diversity of habitats than lowland areas, due to both physical and historical factors (Gentry, 1982, 1995; Young, 1995). Additionally, apparently related species of *Palicourea* frequently show distinct elevational zonation (see discussion of *P. ovalis* and related species, below), further partitioning montane habitats, as noted by Webster (1995).

The relative youth of these areas may also be a factor contributing to high species diversity. Although mountains have existed in the region of the Andes since at least the Eocene (Taylor, 1995), the great height and perhaps also the pluvial climate of the northern Andes are apparently more recent, with the principal uplift occurring during the last 5 million years (van der Hammen, 1974). Significant alteration in local conditions and therefore plant communities has been noted during at least the last 3.5 million years (Hooghiemstra & Cleef, 1995), which suggests that many populations of *Palicourea* have long occupied a changing environment. *Palicourea* has not been reported from fossil assemblages and probably will not be found because of its limited pollen exine, so its historical occurrence is unknown. Modern species of *Palicourea* show variation among populations in flower size (Sobrevila et al., 1983), inflorescence color, and local flowering time (pers. obs., Puerto Rico, Costa Rica), which may favor selection for reproductive isolation through differing phenology and perhaps pollinators. Fragmentation and isolation of montane populations of *Palicourea* species would reinforce this reproductive isolation, while distyly would continue to promote outcrossing among individuals within small populations. Most species of *Palicourea*, including many of those known only from a few widely separated sites, are represented on herbarium specimens by both long-styled and short-styled plants. Only a very few cases of loss of this feature have been demonstrated, mostly in plants of the Antilles (Taylor, 1989), and in populations peripheral to the principal range of the generally distylous species (Sobrevila et al., 1983). Widespread maintenance of distyly in the genus suggests that this feature is adaptive and maintained through selection, and that pollen transfer among plants is effective in most species at least through the principal part of their range.

Many species of *Palicourea* are notoriously similar vegetatively and in fruit, sometimes to the degree that they can be separated only by their mature flowers. Sympatric assemblages of *Palicourea* are common, with the sympatric species usually separated reproductively by phenology and perhaps subtle to marked differences in morphology (e.g., Sobrevila et al., 1983). For example, *Palicourea crocea* (Sw.) Roem. & Schult. and *P. croceoides* Ham. frequently grow sympatrically in Puerto Rico, with plants of both species often found side by side in mixed populations. These species have been treated by a number of authors as conspecific (e.g., Liogier & Martorell, 1982). In one site in Puerto Rico where these species are sympatric, plants of *P. crocea* are usually less than 1 m tall, bear dark red corollas that are shorter than those of *P. croceoides* on yellow inflorescence branches, flower for a period of 1–2 weeks once or twice a year, and are diploid; plants of *P. croceoides* are taller, bear longer yellow corollas on red inflorescence branches, produce flowers during a period of a month or more approximately every 3–4 months, and are polyploid (Taylor, pers. obs.; Kiehn, 1986). Individual plants are difficult to identify to species when not in flower, but the two populations are reproductively isolated and clearly separable by reproductive features, and are considered separate species here. Such reproductive isolation among sympatric *Palicourea* species is probably common; little work has been done in this area.

The relatively greater diversification of *Palicourea* in montane habitats is likely due also in part to its exploitation of hummingbirds as pollinators. An increase in importance of species pollinated by hummingbirds at higher elevations has been noted in surveys covering various families (Webster, 1995), which suggests that this mode of pollination

is more effective than insect pollination at higher elevations. This is probably partly why with increasing elevation, *Palicourea* becomes relatively more important than, or even replaces, *Psychotria* subg. *Heteropsychotria*, the group most closely related to it, which is generally pollinated by small insects.

Character Patterns in *Palicourea*

Diagnostic morphological characters used here to distinguish species of *Palicourea* include the following features. **Stipule form** may be sheathing, i.e., united around the stem in a continuous, usually truncate sheath, or laminar, i.e., with the interpetiolar portion well developed and the intrapetiolar portion reduced or absent; the stipule lobes may be broadly rounded or acute to obtusely angled, and straight at the base or rounded to lobed or subauriculate on one or both sides. **Leaf arrangement** may be paired or occasionally verticillate. **Inflorescence shape** ranges from pyramidal, in most species, to elongated and cylindrical or spiciform, or to rounded-corymbiform with the basal branches ascending and nearly as well as to better developed than the central axis. **Inflorescence** and **corolla colors** may be pale green to white, or dull to bright yellow, orange, red, purple, violet, or blue; corolla color may be similar to or contrast with the inflorescence branches. In general, most species with brightly colored inflorescences or corollas vary from yellow to red, or purple to blue; relatively few species combine colors from these two groups. **Calyx limb length** varies from relatively short, 0.2–1.2 mm long, as in most species of *Psychotria* subg. *Heteropsychotria*, to relatively well developed, to 20 mm long in *Palicourea bella* and related species. **Corolla shape** varies from somewhat swollen and a little gibbous at the base and generally straight there and in the tube, to strongly gibbous at the base, bent to 90° just above this swelling, and curved in the tube; the tube may be slender to relatively stout. **Corolla length** varies from relatively short in the tube, 4–5 mm long, to ca. 40 mm long in species of several different groups; the length of the lobes varies, but generally it is similar in proportion to the length of the tube. Linear **corolla lobe appendages** and **colored multicellular corolla trichomes** are found in a few species. **Fruit shapes** described here are evident mainly on dried specimens and are due to the aggregate shape of the pyrenes. Dried fruits range from subglobose to ellipsoid or obovoid and may sometimes be laterally flattened. **Pyrene number** is typically 2, but ranges to 4–5 in a few species; this number may be constant or variable within a species. The longitudinal **pyrene ridges** may be rounded to nearly flat or raised and sharp.

Characters that may vary within an individual species include general shape and apex (i.e., rounded vs. obtuse or acute) of the calyx lobes; density of the pubescence on vegetative and sometimes reproductive structures (e.g., see discussion of *Palicourea alpina* in Taylor, 1993); color of the inflorescences and corollas, within the general color groups noted above; length of the stipules and pedicels (at least to some extent); and external pubescence of the corolla, including presence or absence of the multicellular colored trichomes. Some morphological structures appear to vary in correlated fashion on individual plants, in particular the proportional widths of leaves, stipule lobes, inflorescence bracts, and calyx lobes are usually similar. Inflorescence and corolla color appear to vary among closely related species and perhaps are correlated with reproductive isolating mechanisms, as in the example of *P. crocea* and *P. croceoides*, above. Among closely related species, for example, three that are morphologically similar have very different inflorescence and corolla colors: *P. ovalis* Standl., found at 1200–2000 m in Colombia and Ecuador, has blue to purple inflorescences and corollas; *P. chimboracensis* Standl., found at 150–1400 m in a similar range, has orange to red inflorescence branches and yellow corollas; and *P. heilbornii* Standl., found at 1400–2200 m only in Pichincha Province, Ecuador, has yellow to orange inflorescence branches and deep red corollas. Species of subgenus *Palicourea* sect. *Grandiflorae* present a similar example: of four similar species, two (*P. grandiflora* (Kunth) Standl., *P. macarthurorum* C. M. Taylor) have red-orange to yellow inflorescences and flowers, while two others (*P. nigricans* K. Krause, *P. amapaensis* Steyerm.) have violet to purple inflorescences and flowers; one yellow-flowered species and one purple-flowered species are sympatric through most of Amazonian South America, in various combinations, while both of the similarly colored species are allopatric.

Several unusual or distinctive features found in one or several species of *Palicourea* are also found in other genera of Rubiaceae, often from other tribes or subfamilies, and thus appear to have been derived more than once in the family. One such feature is a spathaceous calyx, which is completely fused in bud and split irregularly by the elongating calyx; this feature is found in *P. spathacea* C. M. Taylor and is also known in other genera, e.g., *Pentagonia* Benth., *Hippotis* Karst. (both Hippotideae),

and *Phellocalyx* Bridson (Gardenieae, African). The calyx lobes of several species of *Palicourea* are somewhat to strongly unequal in length on an individual flower; this feature is notable in *Palicourea mexiae* Standl., *P. gomezii* C. M. Taylor, *P. gibbosa* Dwyer, *P. discolor* K. Krause (all subg. *Montanae*), *P. fastigiata, P. cymosa* (Ruiz & Pav.) DC. (both subg. *Palicourea*), and other species, and also in some species of *Rondeletia* L. (Rondeletieae), *Pentas* Benth. (Hedyotideae), and many other genera. Verticillate leaves are found in several species of subgenus *Palicourea,* including *P. triphylla* DC., *P. officinalis* Mart., and the species of section *Corymbiferae,* and also in species of *Duroia* L.f. (Gardenieae), *Remijia* DC. (Cinchoneae), *Declieuxia* Kunth (Psychotrieae), *Bathysa* C. Presl, *Rondeletia* (both Rondeletieae), and other genera. Parallel (or convergent) derivation of distinctive conditions can be outlined for additional characters including capitate inflorescences with well-developed bracts, well-developed slender white corollas, and relatively large pyrenes.

Within *Palicourea,* the diagnostic characteristics noted above as used to distinguish species are distributed among the individual species in various—for some features, nearly all possible—combinations. This distribution of character states suggests that at least some of these features have been derived more than once, in some cases apparently several times. Within the classification presented here, characters that have apparently originated more than once include the following:

♦ Multicellular, elongated, colored trichomes on the exterior of the corolla are found in a number of species with inflorescences and flowers of both color groups, including *Palicourea lachnantha* Standl. and *P. mansoana* (Müll. Arg.) Standl. of subgenus *Palicourea,* and *P. thermydri* J. H. Kirkbr., *P. rigidifolia* (Dwyer & M. V. Hayden) Dwyer, *P. eriantha* DC., *P. dorantha* Wernham, *P. justicioides* Standl., *P. calycina* Benth., and *P. cornigera* C. M. Taylor, of several different series in subgenus *Montanae* sect. *Montanae.*

♦ Distinctive obovoid, laterally somewhat flattened fruits are found in a number of species of subgenus *Montanae,* including the species of section *Obovoideae* series 5, which have stipules with truncate continuous sheaths separating the lobes, and the species of section *Obovoideae* series 6, which have laminar stipules with the lobes closely set on each side of a narrow, acute to concave sinus. Thus, either fruit shape is a shared character and stipule form variable among these species, or the distinctive fruit shape has arisen at least twice in these groups while the stipule form has been derived only once.

♦ The form of the longitudinal pyrene ridges is distinctive for several species and useful in separating some species groups. The pyrenes of most species have rounded, usually rather low ridges, but relatively sharp, pronounced ridges seem to have arisen independently in such species as *Palicourea lachnantha* and *P. calophylla* DC., which belong to two different sections of subgenus *Palicourea,* and in the species of subgenus *Montanae* sect. *Cephaeloides* series 10 and section *Montanae* series 4 subseries g.

♦ Calyx length shows marked variation throughout the genus, and to some degree within each species group. It is most variable among species of subgenus *Montanae.* Relatively long calyx limbs seem to have arisen several times in the genus, in *P. cymosa* of subgenus *Palicourea,* and in subgenus *Montanae* in species such as *P. orosiana* C. M. Taylor, *P. chignul* C. M. Taylor (both section *Obovoideae*), and the species of section *Cephaeloides.*

♦ Perhaps the most striking example of a feature that has arisen more than once is the linear corolla lobe appendages found in *P. rigidifolia, P. denslowiae* J. H. Kirkbr., *P. lehmannii* (Rusby) Standl., *P. corniculata* C. M. Taylor, and *P. cornigera* C. M. Taylor, which are all purple- to blue-flowered species of the western Andean cordillera of Colombia and Ecuador. These appendages differ morphologically: the first four species bear a single appendage originating from the middle of the abaxial surface of the corolla lobe (Fig. 9D, E), which is developed to various degrees in the different species and which is found in other species of Psychotrieae and other tribes; whereas *P. cornigera* bears two appendages per lobe, one originating from each side of the base of the lobe (Fig. 9B), an apparently unique feature in the family.

These combinations of morphological characters indicate that at least some of them have been derived more than once. They may suggest also the possibility that the classification proposed here should be reordered; however, any reordering will indicate the repeated derivation of other features, which suggests that the repeated origin of at least some of them is a real occurrence. This in turn suggests that different species may be responding in similar ways to similar patterns of selection in the environment. Particularly suggestive of this last possibility is the repeated similar variation in inflorescence and corolla colors (green and white, yellow-orange-red group, and purple-blue group) with-

in many species groups; the repeated derivation of relatively long, colored calyx limbs; and the unusual, prominent linear corolla lobe appendages described above. In this last case, convergent occurrence of unusual structures that are morphologically distinct suggests that some aspect of the environment of this particular region favors these structures.

An Infrageneric Classification of *Palicourea*

The scheme presented below is based on a survey of the entire genus and monographic work on part of it. It classifies 188 species. This scheme does not include all species in this genus: those not included either have not been studied in adequate detail or are as yet too poorly known for classification. Synonyms at the species level are not included here, but can be found on the World Wide Web at http://www.mobot.org/MOBOT/Staff/Research/taylor/palihome.html. Species included in this classification that are described in this article are indicated with an asterisk. Geographic distributions presented for the species are approximate. "Amazonia" is used here in the sense of Takhtajan's (1986) "Amazonian Region" (i.e., including the Orinoco and other non-Amazonian drainages of lowland, moist to wet, eastern to central South America). Previously published infrageneric taxa of *Palicourea* are included here. Most of the infrageneric taxa subordinate to section that are proposed here are informal; formal description of these and phylogenetic analyses will depend on the completion of monographic work.

This scheme suffers the limitations inherent in translating what is clearly a branched pattern to a linear list. Species are listed in an order that attempts to place similar and apparently closely related species together.

Palicourea Aubl., Hist. pl. Guiane 172, t. 66. 1775. TYPE: *Palicourea guianensis* Aubl.

Subgenus I. Palicourea. Leaves paired to verticillate, usually membranaceous to papyraceous, or subcoriaceous in species of savanna habitats, usually minutely pustulose abaxially; stipules united around the stem into a continuous sheath, this often reduced, the lobes reduced to well developed or obsolete; inflorescences and flowers variously colored; corollas tubular to somewhat funnelform, somewhat to strongly swollen and gibbous at base, generally straight to somewhat bent here and in tube, externally glabrous or pubescent, sometimes with colored multicellular trichomes; pyrenes 2–5 per fruit. Generally found at lower elevations, 0–1200(1500) m, throughout the range of the genus.

Section A. Palicourea.

Psychotria sect. *Oribasia* Müll. Arg., in Mart., Fl. bras. 6(5): 223. 1881. *Palicourea* sect. *Oribasia* (Müll. Arg.) K. Schum., in Engl. & Prantl, Nat. Pflanzenfam. 4(4): 115. 1891. TYPE: *Palicourea grandifolia* (Willd. ex Roem. & Schult.) Standl., lectotype, here designated. Note: Authorship of section *Oribasia* is here ascribed solely to Müller, although he intended to base his name on *Oribasia* Schreb., Gen. pl. 124. 1789, nom. illeg., nom. superfl. for *Palicourea* Aubl.

Palicourea sect. *Stephanium* Griseb., Fl. Brit. W. I. 346. 1861. TYPE: *Palicourea guianensis*. Note: Authorship of section *Stephanium* is here ascribed solely to Grisebach; in the publication of the section, Grisebach referenced *Stephanium* Schreb., Gen. pl. 124. 1789, nom. illeg., which is a nom. superfl. for *Nonatelia* Aubl. and therefore nomenclaturally not synonymous with *Palicourea*, although as originally circumscribed it included *P. guianensis* as well.

Palicourea ser. *Suberosae* (Müll. Arg.) K. Schum., in Engl. & Prantl, Nat. Pflanzenfam. 4(4): 115. 1891. *Psychotria* ser. *Suberosae* Müll. Arg., in Mart., Fl. bras. 6(5): 227. 1881. TYPE: *Palicourea rigida* Kunth.

Psychotria ser. *Paniculatae* Müll. Arg., in Mart., Fl. bras. 6(5): 228. 1881. TYPE: *Psychotria sellowiana* DC., lectotype, here designated, = *Palicourea guianensis*.

Leaves paired; stipule lobes ligulate, usually obtuse to rounded, relatively well-developed; inflorescences pyramidal to broadly so; pyrenes 2–5. One widespread species, Mexico and Antilles to Bolivia and southern Brazil, the remaining species Amazonian.

P. guianensis Aubl. Lowlands of Mexico and Antilles to southern Brazil and Bolivia; pyrenes 2–5 per fruit.

P. grandifolia Kunth. Amazonia; similar to *P. guianensis* and perhaps not actually distinct; pyrenes 4–5 per fruit.

P. buntingii Steyerm. Venezuela; perhaps not distinct from *P. guianensis*.

P. tepuicola Steyerm. Venezuela; perhaps not distinct from *P. guianensis*.

P. rigida Kunth. Pyrrhophytic; savannas throughout South America.

P. semirasa Standl. Middle elevations, Venezuela and Colombia.

P. flavifolia (Rusby) Standl. Middle elevations, Bolivia.

P. attenuata Rusby. Middle elevations, Bolivia.

P. mansoana (Müll. Arg.) Standl. Western Amazonia.

P. lasiantha K. Krause. Western Amazonia.

P. pachycalyx Standl. Western Amazonia; similar to *P. lasiantha*, perhaps not distinct from it.

P. lachnantha Standl. Western Amazonia; characteristically drying turquoise-black, perhaps an aluminum accumulator.

P. anianguana C. M. Taylor*. Local in eastern

Ecuador; combines characters of *P. lachnantha* and *P. lasiantha.*

Section B. Grandiflorae, sect. nov. TYPE: *Palicourea grandiflora* Kunth.

Folia lobis stipularum reductis. Fructus magnitudinem mediam generis aliquantum ad valde excedens.

Leaves paired; stipule lobes relatively reduced, triangular to deltoid or shortly ligulate; inflorescences broadly pyramidal to corymbiform-rounded; fruit somewhat to markedly larger than average, 4–15 mm long; pyrenes 2. Amazonia.

P. grandiflora Kunth. Amazonia.
P. amapaensis Steyerm. Northeastern Amazonia.
P. nigricans K. Krause. Western Amazonia; similar to and perhaps a western sister species to *P. amapaensis.*
P. macarthurorum C. M. Taylor. Western Amazonia, low to middle elevations.

Section C. Crocothyrsae Griseb., Fl. Brit. W. I. 345. 1861. TYPE: *Palicourea crocea* (Sw.) Roem. & Schult., lectotype, here designated.

Leaves paired or verticillate; stipule lobes deltoid to narrowly triangular or lanceolate, acute, rather short to well developed; inflorescences pyramidal to broadly so, corymbiform-rounded to fastigiate or spiciform (series 1) or to narrowly pyramidal (series 2); pyrenes 2. Mexico and Antilles to Paraguay and Bolivia.

Series 1. Croceae (Müll. Arg.) K. Schum., in Engl. & Prantl, Nat. Pflanzenfam. 4(4): 115. 1891. *Psychotria* ser. *Croceae* Müll. Arg., in Mart., Fl. bras. 6(5): 228. 1881. TYPE: *Palicourea crocea,* lectotype, here designated.

Inflorescences pyramidal to broadly so, corymbiform-rounded, fastigiate, or spiciform.

Subseries a. Subcymosae (Müll. Arg.) C. M. Taylor, stat. et comb. nov. Basionym: *Psychotria* ser. *Subcymosae* Müll. Arg., in Mart., Fl. bras. 6(5): 229. 1881. TYPE: *Palicourea barraensis* Müll. Arg., lectotype, here designated, = *P. longiflora* (Aubl.) Rich.

Stipule lobes triangular to narrowly so. Mexico and Antilles to Paraguay and Bolivia.

P. croceoides Ham. Antilles, and perhaps throughout lowland moist South America; this and the next two species comprise a poorly understood, variable, widespread complex of forms that are most diverse in Amazonia.
P. crocea (Sw.) Roem. & Schult. Mexico to Paraguay and Bolivia.
P. fastigiata Kunth. Swamps and edges of blackwater rivers, lowland South America.
P. charianthema Standl. Northern Amazonia.
P. subspicata Huber. Western Amazonia.
P. herzogii Standl. Middle elevations, Bolivia, perhaps to Peru or Ecuador.
P. huberi Steyerm. Guayana Highlands.
P. lancigera Steyerm. Guayana Highlands.
P. longiflora (Aubl.) Rich. Northern and eastern Amazonia.
P. maregravii A. St.-Hil. Eastern Amazonia.
P. coriacea Mart. Savannas of eastern South America, pyrrophytic.
P. mello-barretoi Standl. Savannas, Brazil; perhaps not distinct from *P. coriacea.*
P. officinalis Mart. Savannas; Brazil.
P. longistipulata (Müll. Arg.) Standl. Amazonia, with marked clinal variation from east to west.
P. bracteosa Standl. Western Amazonia.
P. lasiophylla Standl. Western Amazonia, to middle elevations.
P. nitidella (Müll. Arg.) Standl. Eastern Amazonia.

Subseries b. Stipule lobes lanceolate. Western Amazonia.

P. conferta (Benth.) Sandw. Western Amazonia.
P. cymosa (Ruiz & Pav.) DC. Western Amazonia.
P. punicea (Ruiz & Pav.) DC. Southwestern Amazonia.
P. iquitoensis K. Krause. Local in northeastern Peru.
P. plowmanii C. M. Taylor. Local in southeastern Peru.
P. jatun-sachensis C. M. Taylor. Northwestern Amazonia.

Series 2. Verticillatae (Müll. Arg.) K. Schum., in Engl. & Prantl, Nat. Pflanzenfam. 4(4): 115. 1891. *Psychotria* ser. *Verticillatae* Müll. Arg., in Mart., Fl. bras. 6(5): 227. 1881. TYPE: *Palicourea triphylla* DC., lectotype, here designated.

Psychotria ser. *Cylindricae* Müll. Arg., in Mart., Fl. bras. 6(5): 228. 1881. TYPE: *Psychotria tabacifolia* Müll. Arg., lectotype, here designated, = *Palicourea macrobotrys* (Ruiz & Pav.) DC.

Inflorescences pyramidal to elongated and narrowly so. One widespread species, Mexico to Bolivia and southern Brazil, the remainder in Amazonia.

P. macrobotrys (Ruiz & Pav.) DC. Southern Amazonia.
P. tetraphylla Cham. & Schltdl. Southeastern Brazil.
P. longepedunculata Gardner. Southern Brazil.
P. calophylla DC. Northern Amazonia.
P. affinis Standl. Southern Amazonia.
P. anisoloba (Müll. Arg.) Boom & M. T. Campos. Central Amazonia.
P. triphylla DC. Mexico and Cuba to Bolivia and southern Brazil; leaves usually verticillate, though consistently paired in Cuba.
P. melheana Jung-Mend. Brazil; very similar to *P. triphylla.*

Section D. Corymbiferae (Müll. Arg.) C. M. Taylor, stat. et comb. nov. Basionym: *Psychotria* ser. *Corymbiferae* Müll. Arg., in Mart., Fl. bras. 6(5): 229. 1881. TYPE: *Palicourea corymbifera* (Müll. Arg.) Standl., lectotype, here designated.

Psychotria ser. *Bracteosae* Müll. Arg., in Mart., Fl. bras. 6(5): 229. 1881. TYPE: *Palicourea virens* (Müll. Arg.) Standl., lectotype, here designated.

Leaves verticillate or occasionally paired; stipule sheaths subtruncate, lobes reduced or obsolete; inflorescences pyramidal to corymbiform-rounded, with floral bracts often well developed; pyrenes 2–5 per fruit. Amazonia.

P. corymbifera (Müll. Arg.) Standl. Amazonia; pyrenes 2–5 per fruit.
P. virens (Müll. Arg.) Standl. Eastern Amazonia; pyrenes 4–5 per fruit.
P. irwinii Steyerm. Northeastern Amazonia; pyrenes 2 per fruit.
P. quadrifolia (Rudge) DC. Amazonia, with marked clinal variation from east to west; pyrenes 2 per fruit.

Subgenus II. Montanae, subg. nov. TYPE: *Palicourea thyrsiflora* (Ruiz & Pav.) DC.

Folia binatim jugata, papyracea chartacea subcoriaceave, abaxialiter plerumque epustulata; stipulis laminaribus vel circum caulem connatis vaginam continuam formantibus.

Leaves paired, usually papyraceous to chartaceous or subcoriaceous, usually not pustulose abaxially; stipules united around the stem in a usually well-developed, continuous sheath with two short to well-developed lobes, or laminar (i.e., interpetiolar) and bilobed to varying degrees; inflorescences and flowers variously colored; corollas tubular to funnelform, somewhat swollen and gibbous at base and generally straight there and in tube, to very strongly gibbous and swollen at base, constricted and strongly bent, to as much as 90°, just above this, and straight to curved in tube, externally glabrous or pubescent with trichomes of various types, including short to long, multicellular, colored trichomes; pyrenes 2(4) per fruit. Generally found at higher elevations, (150)1000–3500 m (to limit of woody vegetation). Greater Antilles, Mexico and Central America to Venezuela and Bolivia.

Section E. Montanae, sect. nov. TYPE: *Palicourea thyrsiflora* (Ruiz & Pav.) DC.

Folia stipulis circum caulem connatis vaginam continuam formantibus. Fructus pyrenis ellipsoideis ovoideis subglobosisve.

Stipules united around the stem in a continuous, usually well-developed and truncate sheath, with lobes triangular to narrowly so or rarely lanceolate; inflorescences pyramidal to narrowly so or sometimes relatively short and few-flowered in species of higher elevations; infructescences typically becoming purple in all species; fruits ellipsoid, ovoid, or subglobose, sometimes laterally flattened. Greater Antilles, Mexico and Central America to Venezuela and Bolivia.

Series 3. Fruits generally ellipsoid to ovoid and laterally flattened. Mexico and Antilles to Venezuela and Bolivia.

Subseries c. Stipules with sheath moderately to well developed or sometimes reduced in species of higher elevations, with lobes triangular to narrowly so, generally persisting with the stipules. Greater Antilles, Mexico and Central America to Venezuela and Bolivia.

P. thyrsiflora (Ruiz & Pav.) DC. Andes of Colombia and Venezuela to Bolivia.
P. padifolia (Willd. ex Roem. & Schult.) C. M. Taylor & Lorence. Mexico to Panama; similar to *P. thyrsiflora.*
P. alpina (Sw.) DC. Greater Antilles; similar to *P. thyrsiflora,* flowers monomorphic (i.e., not distylous).
P. eriantha DC. Hispaniola; similar to *P. alpina,* flowers monomorphic.
P. angustifolia Kunth. Costa Rica to Venezuela and Peru.
P. rigidifolia (Dwyer & M. V. Hayden) Dwyer. Panama to western Colombia; provisionally placed in *Palicourea,* similar in several features to *P. angustifolia* and perhaps *P. densa* Standl. (Series 4, Subseries f)
P. weberbaueri K. Krause. Colombia to Peru; perhaps a color variant of *P. thyrsiflora.*

P. leucantha Donn. Sm. Guatemala.
P. acetosoides Wernham. Western Colombia.
P. lutulenta Standl. Colombia.
P. heterantha Standl. Colombia; perhaps not distinct from *P. lutulenta.*
P. canarina C. M. Taylor.* Ecuador; similar to *P. thyrsiflora.*
P. subalata Standl. ex Steyerm. Colombia to Peru.
P. gentryi C. M. Taylor.* Local in east-central Ecuador; similar to *P. subalata.*
P. subalatoides C. M. Taylor.* Ecuador; similar to *P. subalata.*
P. danielis Standl. Local in northwestern Colombia.
P. luteonivea C. M. Taylor.* Southern Colombia to Ecuador; similar to *P. thyrsiflora.*
P. holmgrenii Standl. Southern Colombia to Ecuador.
P. vulcanalis Standl. ex C. M. Taylor.* East-central Ecuador.
P. ulloana C. M. Taylor.* Ecuador to northern Peru; pyrenes 4.
P. calothyrsus K. Schum. Ecuador; perhaps a high-elevation form of *P. thyrsiflora.*
P. pennellii Standl. Colombia; perhaps not distinct from *P. calothyrsus.*
P. calantha Standl. Ecuador.
P. ponasae K. Krause. Peru.
P. psittacorum Standl. Colombia to Ecuador.
P. ionantha Standl. Colombia.
P. herrerae Standl. Peru to Bolivia.
P. lobbii Standl. Ecuador.
P. subtomentosa (Ruiz & Pav.) C. M. Taylor.* Ecuador to Bolivia, with marked variation from north to south.
P. buchtienii Standl. Bolivia; provisionally placed here.
P. corniculata C. M. Taylor.* Northern Ecuador.
P. anderssoniana C. M. Taylor.* Ecuador.

Subseries d. Stipules with sheaths well developed, with lobes narrowly triangular to setaceous and usually deciduous to caducous, or obsolete. Ecuador and perhaps Peru.

P. flavescens Kunth. Ecuador and perhaps Peru.
P. tectoneura K. Schum. & K. Krause. Ecuador.
P. prodiga Standl. ex C. M. Taylor.* Central Ecuador.

Series 4. Fruits generally subglobose to ovoid, not laterally flattened. Costa Rica to Venezuela and Bolivia.

Subseries e. Corollas tubular to somewhat funnelform, externally glabrous or pubescent with relatively short, usually colorless trichomes. Costa Rica and Venezuela to Peru.

P. amethystina (Ruiz & Pav.) DC. Colombia to Peru.
P. brenesii Standl. Costa Rica; similar to *P. amethystina.*
P. purpurea C. M. Taylor. Costa Rica and Panama.
P. demissa Standl. Venezuela and Colombia to Ecuador.
P. ovalis Standl. Western Colombia to Ecuador; similar to *P. chimboracensis* and *P. heilbornii.*
P. chimboracensis Standl. Western Colombia to Ecuador; similar to *P. ovalis* and *P. heilbornii.*
P. heilbornii Standl. Local in Ecuador; similar to *P. ovalis* and *P. chimboracensis.*
P. latifolia K. Krause. Colombia to Peru; similar to *P. amethystina.*
P. discolor K. Krause. Costa Rica and Panama; similar to *P. latifolia.*
P. deviae C. M. Taylor.* Ecuador to western Colombia.
P. perquadrangularis Wernham. Venezuela to Colombia.
P. stipularis Benth. Western Colombia to Peru.
P. albert-smithii Standl. Eastern Colombia to Venezuela; similar to *P. stipularis.*
P. lehmannii (Rusby) Standl. Local in western Colombia; provisionally placed here.

Subseries f. Calyx relatively well developed; corollas tubular, often relatively well developed, externally glabrous to pubescent with short colorless trichomes or sometimes with multicellular, colored, showy trichomes. Central America to northern Ecuador.

P. heterochroma K. Schum. & K. Krause. Western Colombia to Ecuador.
P. albocaerulea C. M. Taylor. Local in Costa Rica.
P. lancifera Standl. & L. O. Williams. Honduras to Costa Rica.
P. macrocalyx Standl. Costa Rica to Panama.
P. standleyana C. M. Taylor. Costa Rica to Colombia.
P. antioquiana Standl. Northwestern Colombia.
P. tunjaensis C. M. Taylor. Colombia.

P. calophlebia Standl. Western Colombia to Ecuador.
P. toroi Standl. Western Colombia.
P. dorantha Wernham. Western Colombia.
P. densa Standl. Western Colombia.
P. justicioides Standl. Western Colombia.
P. calycina Benth. Local in Ecuador.
P. azurea C. M. Taylor.* Local in Ecuador.
P. jaramilloi C. M. Taylor.* Southern Ecuador.
P. cornigera C. M. Taylor.* Southern Ecuador.

Subseries g. Inflorescences pyramidal to broadly so or corymbiform-rounded, usually with floral bracts relatively well developed and broad; corollas tubular, with tubes relatively stout; pyrenes generally triangular in cross section. Western Colombia to Peru.

P. quadrilateralis C. M. Taylor. Northwestern Colombia (in press, *Novon*).
P. thermydri J. H. Kirkbr. Northwestern Colombia.
P. denslowiae J. H. Kirkbr. Local in northwestern Colombia.

Section F. Obovoideae, sect. nov. TYPE: *Palicourea hospitalis* Standl.

Folia stipulis laminaribus vel circum caulem connatis vaginam continuam formantibus. Fructus plerumque obovoideus etiam lateraliter subcomplanatus.

Stipules united around the stem in a continuous sheath or laminar; corollas generally funnelform, somewhat to strongly gibbous at base, slightly to strongly constricted and bent there, externally glabrous or pubescent with usually colorless trichomes; fruit generally obovoid and somewhat flattened laterally. Costa Rica to Venezuela and Ecuador.

Series 5. Stipules united around the stem in a continuous truncate sheath; inflorescences generally yellow, or sometimes flushed with purple or blue, generally remaining or becoming yellow in fruit. Costa Rica to northwestern Colombia or perhaps Ecuador.

P. lasiorrhachis Oerst. Costa Rica to northwestern Colombia.
P. pendula C. M. Taylor. Local in Panama.
P. vestita Standl. Local in Costa Rica.
P. obtusata K. Krause. Venezuela.
P. orosiana C. M. Taylor. Local in Costa Rica and western Panama.
P. chiriquina Standl. Local in western Panama.
P. montivaga Standl. Costa Rica, perhaps to western Panama.
P. adusta Standl. Costa Rica, perhaps to western Panama.

Series 6. Stipules laminar; inflorescences yellow to orange or red, often becoming purple in fruit. Panama to Ecuador.

P. hospitalis Standl. Western Colombia to Ecuador.
P. sodiroi Standl. Local in Ecuador; perhaps not distinct from *P. hospitalis*.
P. chignul C. M. Taylor.* Northwestern Ecuador.
P. kalbreyeri Standl. Western Colombia to Ecuador.
P. lugoana C. M. Taylor.* Western Colombia to Ecuador.
P. asplundii C. M. Taylor.* Ecuador.
P. gibbosa Dwyer. Panama to Ecuador.
P. lyristipula Wernham. Colombia to Ecuador.
P. myrtifolia K. Schum. & K. Krause. Ecuador.

Series 7. Stipules laminar; inflorescences pyramidal to corymbiform-rounded, variously colored in flower and fruit; pyrenes with ridges rounded and often becoming planar to nearly smooth at maturity. Panama to Venezuela and Ecuador.

P. apicata Kunth. Venezuela and Colombia to Ecuador.
P. andaluciana Standl. Western Colombia to Ecuador.
P. sulphurea (Ruiz & Pav.) DC. Peru, perhaps north to Colombia.
P. vaginata Benth. Colombia and Venezuela; identity not clear, provisionally recognized here.
P. tubuliflora Dwyer. Panama.
P. tumidonodosa Dwyer. Panama, perhaps to northwestern Colombia.
P. salicifolia Standl. Costa Rica to western Panama.
P. pauciflora Standl. Local in Costa Rica and western Panama; provisionally placed here, fruit unknown.
P. nubigena Standl. Western Colombia, perhaps to Peru.
P. mexiae Standl. Costa Rica to Peru.
P. gomezii C. M. Taylor. Costa Rica to Ecuador.
P. amplissima (Standl. ex Steyerm.) C. M. Taylor. Western Colombia.

Section G. Pseudoamethystinae, sect. nov. TYPE: *Palicourea obovata* (Ruiz & Pav.) DC.

Folia stipulis laminaribus. Fructus ex subgloboso ovoideus, lateraliter nec complanatus.

Stipules laminar; inflorescences pyramidal; inflo-

rescences and flowers blue to purple; corollas with relatively well developed tubes; fruits subglobose to ovoid, not laterally flattened. Western Colombia to Peru.

P. lineata Benth. Colombia to Peru; similar to *P. stipularis* but with stipules laminar.
P. obovata (Ruiz & Pav.) DC. Colombia to Peru; similar to *P. latifolia* but with stipules laminar.
P. subscandens Standl. ex Steyerm. Western Colombia to Peru; similar to *P. perquadrangularis* but with stipules laminar.

Section H. Psychotrioides, sect. nov. TYPE: *Palicourea petiolaris* Kunth.

Folia stipulis laminaribus. Fructus plerumque ellipsoideus etiam lateraliter complanatus.

Stipules laminar; inflorescences pyramidal to broadly so or rounded-corymbiform, frequently yellow or sometimes pink; corollas yellow to white or pink; fruit generally ellipsoid and distinctly flattened laterally. Mexico and Costa Rica to Venezuela and Ecuador.

Series 8. Corollas with tubes relatively short. Costa Rica and Venezuela to Ecuador and in Jamaica.

P. petiolaris Kunth. Venezuela to eastern Colombia.
P. leuconeura Standl. Venezuela to eastern Colombia.
P. steyermarkii C. M. Taylor. Venezuela.
P. tilaranensis C. M. Taylor. Costa Rica.
P. garciae Standl. Costa Rica to Ecuador.
P. jahnii Standl. Venezuela, perhaps to Colombia.
P. caloneura Rusby. Local in northeastern Colombia.
P. abbreviata Rusby. Local in northeastern Colombia.
P. zarucchii C. M. Taylor. Northwestern Colombia (in press, *Novon*).
P. pittieri Standl. Venezuela and eastern Colombia.
P. pulchra Griseb. Jamaica; provisionally placed here.
P. wilesii C. D. Adams. Jamaica; similar to *P. pulchra*.
P. aschersonianoides (Wernham) Steyerm. Venezuela to eastern Colombia.

Series 9. Inflorescences corymbiform-rounded; corollas with relatively long tubes, these often elongating shortly before anthesis from relatively short buds. Southern Mexico and Venezuela to Ecuador.

P. linearifolora Wernham. Venezuela to eastern Colombia.
P. macrantha Loes. Southern Mexico; provisionally placed here.
P. boyacana Standl. Eastern Colombia.
P. andrei Standl. Colombia to northern Ecuador.
P. candida C. M. Taylor.* Northern Ecuador.

Section I. Cephaeloides, sect. nov. TYPE: *Palicourea bella* (Standl.) Dwyer.

Folia stipulis laminaribus. Inflorescentia bracteis et limbo calycino modice vel bene evolutis.

Stipules laminar; inflorescences pyramidal to broadly so or corymbiform-rounded, or congested to subcapitate, usually pink to red-purple; usually with relatively well-developed and showy bracts; calyx limb moderately to very well developed; corollas tubular to somewhat funnelform, usually white to purple, often with tubes relatively well developed. Costa Rica to Ecuador.

Series 10. Inflorescences pyramidal to corymbiform-rounded; calyx moderately to well developed, usually colored and showy; pyrenes generally relatively large, with ridges relatively sharp and well developed. Costa Rica to western Colombia.

P. bellula C. M. Taylor. Costa Rica.
P. stenosepala Standl. Western Colombia to Ecuador.
P. bella (Standl.) Dwyer. Costa Rica to Panama.
P. spathacea C. M. Taylor. Local in Costa Rica.
P. hammelii C. M. Taylor. Costa Rica to Panama.
P. killipii Standl. Local in western Colombia.
P. ochnoides Dwyer. Western Panama.

Series 11. Stipules often relatively large; inflorescences congested to subcapitate, with bracts usually well developed and showy; pyrenes generally not unusually large, with ridges rounded and frequently low. Panama and Venezuela to Peru.

P. grandistipula (Standl. ex Steyerm.) C. M. Taylor. Western Colombia.
P. macbridei Standl. Peru.
P. condorica C. M. Taylor.* Southern Ecuador.
P. harlingii C. M. Taylor.* Northeastern Ecuador.
P. tamaensis (Standl. & Steyerm.) Steyerm. Venezuela and Colombia.
P. skotakii C. M. Taylor. Local in Costa Rica.
P. sopkinii C. M. Taylor. Western Colombia (in press, *Novon*).

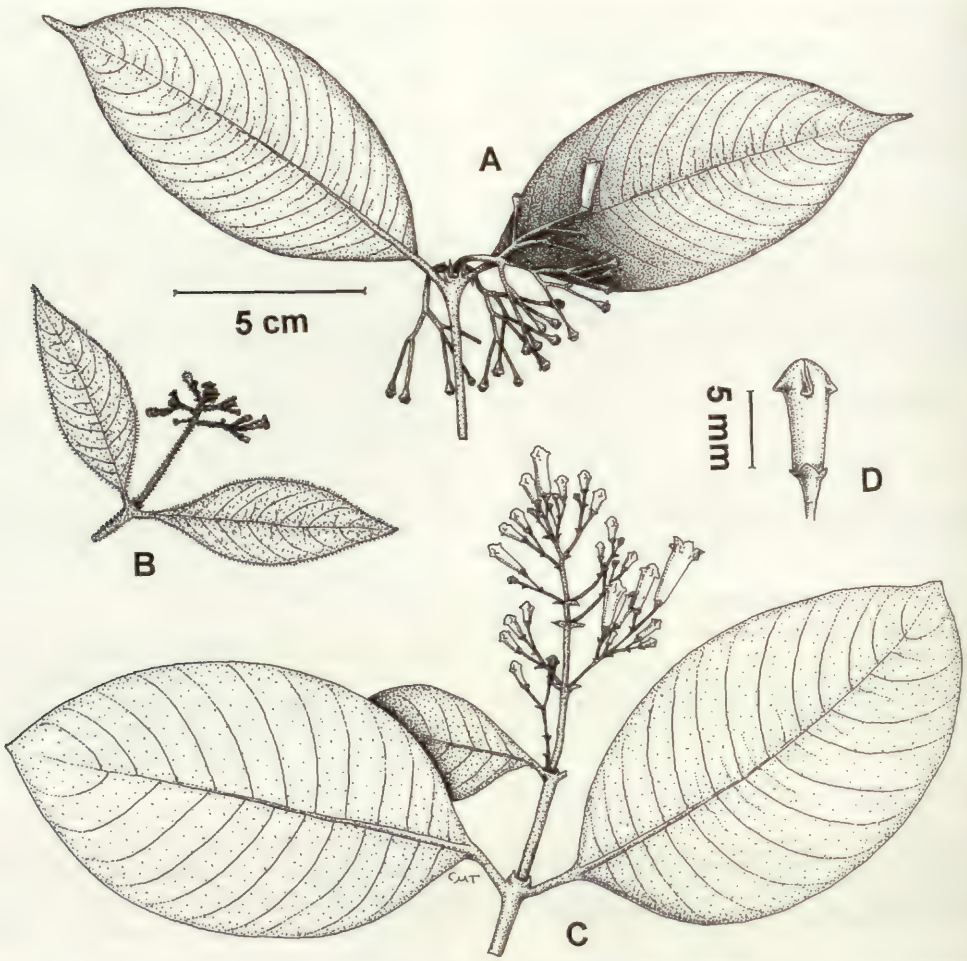

Figure 2. —A. *Palicourea anderssoniana*, flowering branch, based on *Asplund 17430*.—B. *Palicourea subtomentosa* subsp. *lojana*, flowering branch, based on *Harling & Andersson 21367*. C, D, *Palicourea canarina*, based on *Harling & Andersson 21825*.—C. Flowering branch.—D. Flower in bud. A–C to 5-cm scale.

P. dimorphandrioides (Dwyer) C. M. Taylor. Eastern Panama to western Colombia.

P. acanthacea C. M. Taylor. Western Panama to northwestern Ecuador.

P. frontinensis Cogollo & C. M. Taylor. Western Colombia (in press, *Caldasia*).

P. orquidea C. M. Taylor. Western Colombia (in press, *Novon*).

Descriptions of New Taxa

The following newly described taxa are included in the infrageneric classification presented above, which indicates their relationships within *Palicourea*. They are treated here in alphabetical order; the position of each species in the infrageneric classification is indicated at the end of the morphological description. Descriptions and diagnostic characters of the genus *Palicourea* have been presented by Taylor (1989) and Burger and Taylor (1993).

Palicourea anderssoniana C. M. Taylor, sp. nov. TYPE: Ecuador. Pichincha: Reserva Florística-Ecológica "Río Guajalito," Km 59 de la carretera antigua Quito-Santo Domingo de los Colorados, a 3.5 km al NE de la carretera, estribaciones occidentales del Volcán Pichincha, 00°13′53″S, 78°48′10″W, 11 Aug. 1985, *J. Jaramillo & V. Zak 7992* (holotype, MO-4990804; isotype, AAU). Figure 2A.

Haec species a congeneris inflorescentiis sessilis ramis imis reflexis, pedicellis sat longis atque corolla lutea gibbosa glabra distinguitur.

Flowering at 1.5 m tall, to 5 m tall; stems glabrous. *Leaves* paired; *blades* elliptic to rather broad-

ly so or oblanceolate, 7–15 × 2.5–8 cm, at apex rather abruptly acuminate with tips 5–15 mm long and usually falcate, at base cuneate to acute, papyraceous to chartaceous, adaxially glabrous, abaxially sparsely to moderately pilosulous, usually markedly more densely so on costa and secondary veins; secondary veins 8–15 pairs, generally extending to margins, with 1–3 weak intersecondary veins usually present between pairs of secondary veins, adaxially venation plane or costa sometimes thickened, abaxially costa and secondary veins prominulous and lesser venation thickened; margins thinly cartilaginous, entire; *petioles* glabrous, 6–25 mm long; *stipules* glabrous, united around the stem in a continuous truncate sheath 2.5–3 mm long, lobes narrowly triangular, 4–5 mm long, acute, ciliolate. *Inflorescences* deflexed, sessile; panicles broadly pyramidal to corymbiform, 6–15 × 6–15 cm excluding corollas, with secondary axes 2–4 pairs, the basalmost pair reflexed, with flowers pedicellate in cymules of 3–7; bracts narrowly triangular, 3–9 mm long, acute, ciliolate, those subtending secondary axes 5–9 mm long, those subtending pedicels 3–5 mm long; pedicels 5–17 mm long; axes, bracts, and pedicels glabrous, yellow to red; *flowers* with hypanthium glabrous, cylindrical, 1–1.3 mm long, *calyx* limb glabrous, 1.5–2 mm long, divided for ¾ to nearly completely to base, lobes triangular to ovate, rounded to acute or slightly acuminate, equal or somewhat unequal on an individual flower, entire; *corolla* tubular to somewhat funnelform, yellow, at base swollen and generally strongly gibbous, generally straight there, straight or slightly curved in tube, externally glabrous or sometimes pilosulous on lobes in bud, internally glabrous except for a densely villous ring ca. 4 mm above the base, tubes 17–19 mm long, 4–5 mm diam. near middle, lobes 3–6 mm long, slightly thickened adaxially at apex; *anthers* in apparent short-styled form partially exserted, ca. 4 mm long; *stigmas* not seen; *disk* ca. 1 mm high. *Infructescences* similar to inflorescences; *fruit* ellipsoid to subglobose, ca. 7 mm diam.; *pyrenes* with 3–5 low, rather sharp longitudinal ridges. Cloud and wet montane forest at 1325–1930 m, north-central Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its sessile inflorescences with the basalmost pair of secondary axes reflexed, relatively long pedicels, and glabrous, gibbous, yellow corollas. This inflorescence arrangement is unique in *Palicourea*. Vegetatively *P. anderssoniana* resembles *P. thyrsiflora*. This handsome plant is named in honor of Swedish botanist Lennart Andersson, whose work has contributed significantly to our understanding of the Ecuadorian flora and its biogeography.

Paratypes. ECUADOR. **Pichincha**: El Volante on road from Chiriboga to Santo Domingo de los Colorados, *Asplund 17430* (S); along road between Tandayapa and Mindo, 19 km from Tandayapa, about 5.5 km from Mindo, *Croat 49391* (MO); cantón Quito, parroquia Mindo, "Bosque Protector Mindo," cumbre de la montaña entre río Mindo y río Bagasal, 00°02′N, 78°48′W, *Delprete et al. 6098* (MO, TEX); Guajalito, carretera antigua Quito-Santo Domingo, 00°10′S, 78°55′W, *Palacios 525* (MO); along new road Nanegal-Mindo, *van der Werff 13397* (MO); Río Guajalito, near Chiriboga, along old Quito-Santo Domingo road, *van der Werff et al. 12214* (MO).

Palicourea anianguana C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: Añangu, Río Napo, 00°31–32′S, 76°23′W, 16–27 Apr. 1983, *J. E. Lawesson, T. Læssøe & P. M. Jørgensen 39442* (holotype, MO-4279338; isotypes, AAU, QCA not seen). Figure 3.

Haec species a congeneris lobis stipularibus bene evolutis ex obtusis rotundatis, inflorescentia purpurea dense pubescente, corolla trichomatibus purpureis longis vestita atque pyrenis acute porcatis distinguitur.

Flowering at 5 m tall, to 8 m tall; stems glabrous to densely puberulous. *Leaves* paired; *blades* elliptic to broadly so, 15–32 × 7–19 cm, at apex shortly acuminate with deltoid tips 5–10 mm long, at base obtuse to truncate or somewhat rounded, membranaceous to papyraceous, adaxially minutely puberulous to glabrous, abaxially moderately to densely short-pilosulous throughout; secondary veins 12–18 pairs, occasionally looping to interconnect in distal part of leaf, without or with 1(2) weak intersecondary veins usually present between pairs of secondary veins, adaxially costa prominulous to prominent, secondary veins thickened to prominulous, and minor venation plane, abaxially costa prominent, secondary veins prominulous, and minor venation plane and not particularly evident; margins thinly cartilaginous, entire; *petioles* puberulous to glabrous, 13–38 mm long; *stipules* glabrous to puberulous, united around the stem in a continuous truncate to concave sheath 1–1.5 mm long, lobes ligulate, 9–13 mm long, obtuse to rounded, ciliolate. *Inflorescences* erect; peduncles 4.5–9 cm long; panicles pyramidal, 4–10 × 4–10 cm excluding corollas, with secondary axes 4–9 pairs, with flowers pedicellate in cymules of 3–7; bracts narrowly triangular to lanceolate or linear, acute, those subtending secondary axes displaced distally for ⅓ to ½ of length of first axis internode, 5–8 mm long, those subtending pedicels 1–3 mm long; pedicels 1–6 mm long; peduncle, axes, bracts, and pedicels

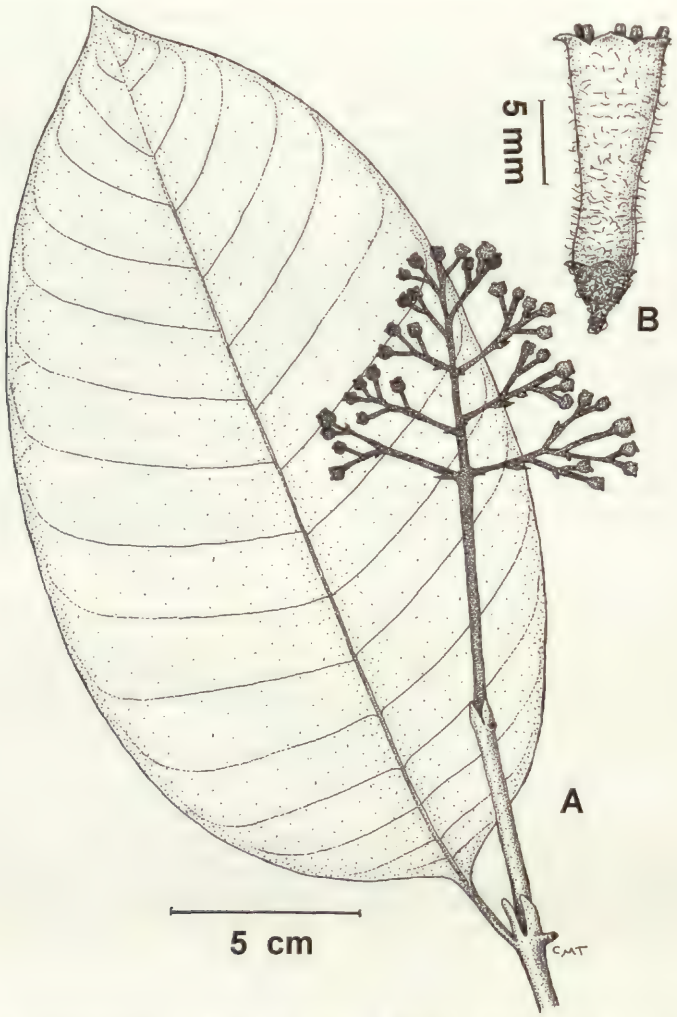

Figure 3. *Palicourea anianguana.*—A. Flowering branch, based on *Balslev et al. 62299.*—B. Flower, based on *Lawesson et al. 39442.*

densely tomentellous or hirsutulous, violet to red; *flowers* distylous, with hypanthium densely lanate, turbinate to cupuliform, 1.5–2 mm long; *calyx* limb 1–1.2 mm long, subtruncate to shallowly lobed, internally glabrous, externally densely lanate; *corolla* tubular to somewhat funnelform, white to violet or pink, somewhat swollen at base, generally straight there and in tube, externally densely pubescent with purple to violet trichomes 1–3 mm long, internally glabrous except for a densely villous ring ca. 2 mm wide at ca. ⅓ of length of tube above base, tube 15–20 mm long, 3–4 mm diam. near middle, lobes triangular to deltoid, 2.5–3 mm long, acute; *anthers* in short-styled form partially exserted, ca. 5 mm long, in long-styled form included, positioned in upper ⅓ of tube, ca. 5 mm long; *stigmas* in short form ca. 3 mm long, positioned near middle of tube, in long form ca. 1.5 mm long, exserted; *disk* 1.5–2 mm long. *Infructescences* red-violet; *fruit* ellipsoid, 8–9 × 7–8 mm, lanate; *pyrenes* with sharp longitudinal ridges. Rainforest in tierra firme at 260–350 m, northeastern Ecuador. [Subg. *Palicourea,* Sect. *Palicourea.*]

This species is distinguished by its stipules with well-developed obtuse to rounded lobes and short, truncate to concave sheaths, thin-textured leaves, well-developed pyramidal purple panicles, densely tomentellous to hirsutulous inflorescence axes, lanate calyces, corollas that are externally pubescent with long purple trichomes, fruit not at all flattened, and pyrenes with sharp longitudinal ridges. It is similar to *Palicourea lasiantha,* which has corollas externally pubescent with trichomes 0.5 mm long

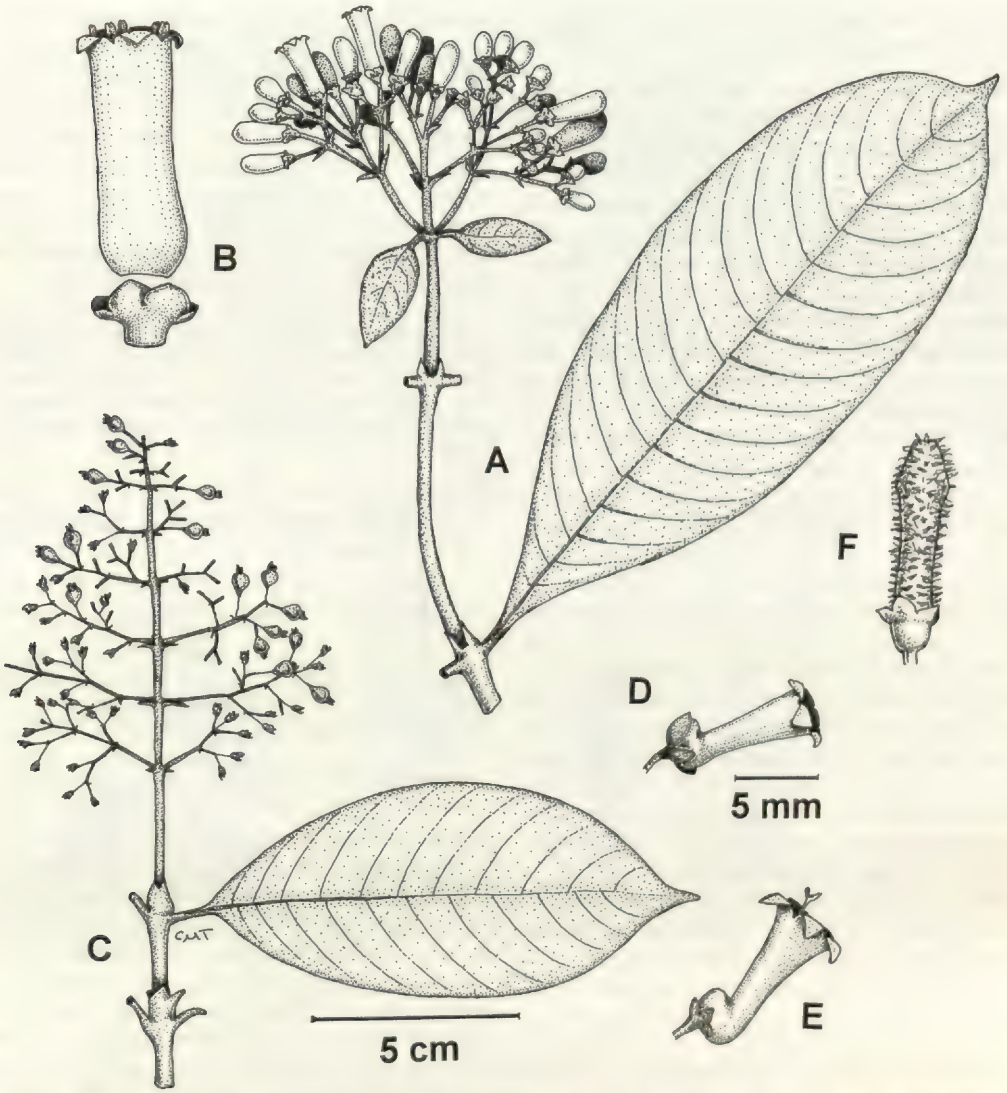

Figure 4. A, B, *Palicourea subalatoides*, based on *Asplund 18928*.—A. Flowering branch.—B. Calyx and corolla, partially dissected. C, D, *Palicourea asplundii*.—C. Flowering branch, based on *Asplund 8672*.—D. Flower, based on *Tipaz et al. 280*.—E. *Palicourea lugoana*, flower, based on *Lugo 14*.—F. *Palicourea gentryi*, flower in bud, based on *Neill 7532*. A, C to 5-cm scale; B, D–F to 5-mm scale.

or shorter and inflorescence branches, calyces, and fruits glabrous to puberulous; and to *P. lachnantha*, which has acute stipule lobes 2–8 mm long, calyx limb 1.8–2 mm long, and pyrenes with rounded ridges. *Palicourea anianguana* combines distinctive characteristics of both *P. lasiantha* and *P. lachnantha*, but it is not intermediate in these features and is consequently here considered a separate, local species. The specific epithet refers to the area where this new species has been collected, Añangu.

Paratypes. ECUADOR. **Napo**: Añangu, S bank of Río Napo 95 km downstream from Coca, 00°32′S, 76°23′W, *Balslev et al. 62299* (AAU); Añangu, NW corner of Parque Nacional Yasuní, 00°32′S, 76°22–23′W, *Korning & Thomsen 47044* (AAU); Añangu, in Parque Nacional Yasuní, 00°31–32′S, 76°23′W, *Øllgaard et al. 39247* (AAU, MO).

Palicourea asplundii C. M. Taylor, sp. nov. TYPE: Ecuador. Carchi: cantón Tulcán, Reserva Indígena Awá, parroquia Tobar Donoso, sector El Baboso, 00°53′N, 78°20′W, 3 Oct. 1991, *G. Tipaz, D. Rubio & M. Taicuz 280* (holotype, MO-4990803; isotype, QCNE not seen). Figure 4C, D.

Haec species a congeneris stipularum interpetiolarium

lobis rotundatis, limbo calycino sat bene evoluto atque corolla flava valde gibbosa curvataque distinguitur.

Flowering at 3 m tall; stems glabrous to hirsutulous. *Leaves* paired; *blades* elliptic, 9.5–23.5 × 4.5–12.5 cm, at apex shortly acuminate with deltoid to slender tips 3–8 mm long, at base cuneate to obtuse, papyraceous, glabrous throughout; secondary veins 13–18 pairs, sometimes uniting with margins in distal part of blade, with 1(3) intersecondary veins usually present between pairs of secondary veins, adaxially and abaxially costa prominulous, secondary veins plane to thickened, and minor venation plane to slightly thickened; margins thinly cartilaginous; *petioles* glabrous to pilosulous, 6–40 mm long; *stipules* glabrous to hirsutulous, laminar, ovate in outline, 7–10 mm long, bilobed for ca. ⅓, lobes rounded to elliptic, often overlapping laterally, ciliolate, with sinus concave to narrowly so. *Inflorescences* erect; peduncles 2.5–4.5 cm long; panicles pyramidal, 9–18 × 8–16 cm excluding corollas, with secondary axes 5–12 pairs, with flowers pedicellate in cymules of 5–9; bracts narrowly elliptic to ligulate, acute to obtuse, entire to ciliolate, those subtending secondary axes 3–11 mm long, those subtending pedicels 0.8–3 mm long; pedicels 1.5–6.5 mm long; peduncle, axes, bracts, and pedicels moderately to densely short-pilosulous, yellow; *flowers* with hypanthium turbinate, glabrous, ca. 1 mm long; *calyx* limb glabrous, 2–2.8 mm long, divided nearly or completely to base, lobes elliptic to lanceolate, triplinerved, minutely ciliolate, obtuse to rounded; *corolla* funnelform, yellow, strongly swollen and gibbous at base, constricted above the swelling, bent there to ca. 90°, generally straight in tube, externally glabrous, internally glabrous except for a narrow pilose ring at the constriction, tube ca. 9 mm long, 1–1.5 mm diam. near middle, lobes deltoid, 1.5–1.8 mm long, acute; *anthers* in long-styled form ca. 1.8 mm long, included, positioned in upper ⅓ of tube; mature *stigmas* not seen; *disk* ca. 0.5 mm high. *Infructescences* similar to inflorescences; *fruit* ellipsoid to usually obovoid, laterally somewhat flattened, ca. 5 × 6 mm; mature *pyrenes* not seen, perhaps with 3–5 somewhat sharp longitudinal ridges. Wet forest at 1600–1800 m, northwestern Ecuador and adjacent Colombia. [Subg. *Montanae*, Sect. *Obovoideae*, Ser. 6.]

This species is distinguished by its laminar stipules with rounded relatively short lobes, yellow inflorescences and flowers, relatively well-developed and deeply divided calyx limb, strongly gibbous and bent corollas, and usually obovoid, laterally somewhat flattened fruits. It is similar to *Palicourea gibbosa* Dwyer, which has stipules divided for half or more of their length with the lobes acute and calyx limb 0.8–1 mm long; to *P. lyristipula*, which has stipules usually divided for half or more of their length with the lobes acute and calyx limbs 1–1.8 mm long; and to *P. lugoana*, which has calyx limbs 0.3–0.9 mm long. The specific epithet honors Swedish botanist Erik Asplund (1888–1974), who first collected this species and who documented the Ecuadorian flora with excellent specimens.

Paratypes. COLOMBIA. **Nariño**: municipio Barbacoas, corregimiento El Divise, *de Benavides 1577* (PSO); municipio Ricaurte, camino los Cruces-Curcuel, *Ramírez et al. 8709* (PSO). ECUADOR. **Pichincha:** Chiriboga, on road from Quito to Santo Domingo de los Colorados, *Asplund 8672* (MO, S).

Palicourea azurea C. M. Taylor, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: Loja-Zamora road at pass, 12 Feb. 1985, *G. Harling & L. Andersson 21999* (holotype, GB; isotype, MO-4278731). Figure 5D, E.

Haec species a congeneris inflorescentia floribusque azureis, floribus pedicellatis sessilibusque admixtis atque tubo corollino 15–17 mm longo extus trichomatibus azureis multicellularibus vestito distinguitur.

Flowering at 1 m tall, to 4 m tall; stems moderately to densely hirtellous becoming glabrescent with age. *Leaves* paired; *blades* elliptic, 4.5–11.5 × 1.8–6.2 cm, at apex acute to shortly acuminate with deltoid tips 5–8 mm long, at base cuneate to obtuse, chartaceous to subcoriaceous, adaxially glabrous except hirtellous along costa, abaxially moderately to densely hirtellous on costa and secondary veins, glabrous to hirtellous on lamina; secondary veins 9–13 pairs, generally extending to unite with margins, with 1(2) distinct intersecondary veins usually present between pairs of secondary veins, adaxially venation plane, abaxially costa prominent, secondary veins prominulous, and reticulated minor venation plane to thickened; margins thinly cartilaginous; *petioles* 5–12 mm long, hirtellous; *stipules* glabrous to hirtellous, united around the stem in a continuous truncate sheath 3–4 mm long, lobes narrowly triangular, 4–5 mm long, acute, entire to ciliolate. *Inflorescences* erect, sometimes tripartite and appearing sessile; peduncles 2–3 cm long; panicles pyramidal, 5–7.5 × 3–5 cm excluding corollas, with secondary axes 4–6 pairs, with flowers sessile and shortly pedicellate together in cymules of 3–7; bracts subtending secondary axes 4–8 mm long, triangular to ligulate or lanceolate, acute to obtuse, ciliolate, those subtending pedicels 2–4 mm long, triangular to narrowly so, acute, ciliolate; pedicels 0–4 mm long; peduncle,

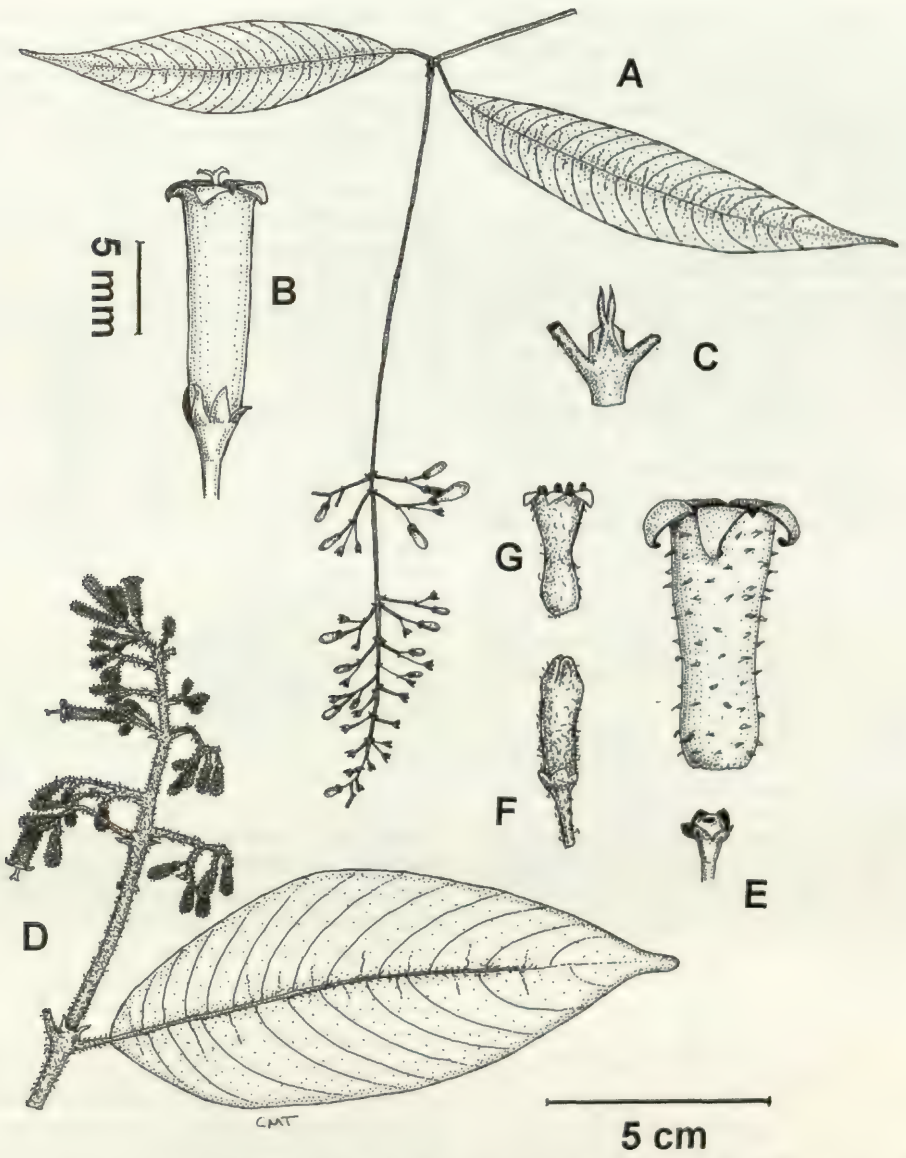

Figure 5. A–C. *Palicourea ulloana*.—A. Flowering branch, based on *Barbour 4161*.—B. Flower, based on *Harling 27144*.—C. Stipule, based on *Barbour 4161*. D, E, *Palicourea azurea*, based on *Madsen 75572*.—D. Flowering branch.—E. Calyx and corolla, partially dissected. F, G, *Palicourea jaramilloi*.—F. Flower in bud, based on *Jaramillo & Winnerskjold 5784*.—G. Corolla at anthesis, based on *Jørgensen et al. 459*. A, D to 5-cm scale; B, C, E–G to 5-mm scale.

axes, bracts, and pedicels blue, moderately to densely hirtellous; *flowers* distylous, frequently pendulous, with hypanthium turbinate, glabrous, ca. 1 mm long; *calyx* limb glabrous to hirtellous, 1–2 mm long, lobed generally to base, lobes lanceolate to triangular, acute, equal to unequal on an individual flower; *corolla* tubular to somewhat funnelform, blue, a little swollen at base, generally straight there and in tube, externally sparsely to densely pubescent with blue multicellular trichomes 0.3–1 mm long, internally glabrous except for a densely pilose ring ca. 2 mm wide at ca. ¼ of length of tube above base, tube 15–17 mm long, 3–5 mm diam. near middle, lobes triangular, 2.5–3.5 mm long, slightly thickened and hooked adaxially; *anthers* in long-styled form ca. 3 mm long, positioned ca. ⅔ of length of tube above base, in short-styled form ca. 3 mm long, partially exserted;

stigmas in long-styled form exserted, ca. 1 mm long, in short-styled form ca. 2 mm long, positioned ca. ⅔ of length of tube above base; disk ca. 0.8 mm high. *Infructescences* and *fruit* not seen. Wet, cloud and elfin forest, to the edge of forest vegetation, at 2550–2950 m, southern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 4, Subser. f.]

This species is distinguished by its truncate sheathing stipules, blue inflorescences and flowers, bracts subtending pedicels and flowers 2–4 mm long, and corollas with tubes 15–17 mm long and externally pubescent with multicellular blue trichomes. The specific epithet refers to the strong blue color of the flowers, even on dried specimens. *Palicourea azurea* is similar to *P. amethystina*, which has bracts subtending flowers and pedicels 1–2 mm long and corollas with tubes 9–15 mm long and externally glabrous or hirtellous with colorless, uniseriate trichomes; and to *P. stipularis*, which has bracts subtending pedicels and flowers 0.5–1.5 mm long, calyx limb 0.8–1.2 mm long, and corolla tubes 2–2.5 mm in diameter and externally glabrous or pubescent with colorless, uniseriate trichomes.

Paratypes. ECUADOR. **Loja**: Parque Nacional Podocarpus, new road Loja-Zamora, E of Cerro Yanococha, 03°59′S, 79°07′W, *Madsen 75572* (AAU); summit of Loja-Malacotos road on Nudo de Cajanuma, 6 mi. S of Loja, *Wiggins 10879* (F). **Zamora-Chinchipe**: Nudo de Sabanilla, just E of the pass on the road to Valladolid, *Harling & Andersson 21517* (GB); limit of Parque Nacional Podocarpus, around pass on road Loja-Zamora, 03°58′S, 79°07′W, *Madsen & Ellemann 75983* (AAU).

Palicourea canarina C. M. Taylor, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: above Valladolid on road to Yangana, 1 Feb. 1985, *G. Harling & L. Andersson 21411* (holotype, GB; isotype, MO-4278929). Figure 2C, D.

Haec species a congeneris stipularum vaginis continuis truncatis ac lobis latis brevibusque, inflorescentia pyramidali atque corollae luteae tubulari-infundibuliformis sinibus (praesertim in alabastro) basi in alas breves aliquam vel bene evolutis distinguitur.

Flowering at 1 m tall, to 5 m tall; stems glabrous. *Leaves* paired; *blades* elliptic, 5.5–20.5 × 2–11 cm, at apex acute to shortly acuminate with tips to 5 mm long, at base acute to usually cuneate or obtuse, papyraceous to chartaceous, adaxially glabrous, abaxially glabrous to sparsely hirtellous or sometimes moderately to densely so along costa; secondary veins 8–12 pairs, usually extending to unite with margins, with 1(3) sometimes weak intersecondary veins usually present between pairs of secondary veins, adaxially costa plane to slightly canaliculate and remaining venation plane, abaxially costa prominulous to prominent, secondary veins prominulous, and reticulated minor venation plane; margins thinly to distinctly cartilaginous; *petioles* 0.5–2 cm long, glabrous; *stipules* glabrous, united around the stem in a continuous truncate sheath 1.5–4 mm long, lobes ligulate to deltoid, 0.5–2 mm long, obtuse to rounded, entire to sparsely ciliolate. *Inflorescences* erect, sometimes tripartite and appearing subsessile; peduncles 1.5–7 cm long; panicles pyramidal, 2–23 × 3–12 cm excluding corollas, with secondary axes 4–8 pairs, with flowers pedicellate in cymules of 3–7; bracts entire to ciliolate, those subtending secondary axes 3–8 mm long, lanceolate to elliptic or narrowly so, acute to obtuse or rounded, entire, those subtending pedicels 1–3 mm long, narrowly to broadly triangular, ovate, or elliptic, acute to obtuse or rounded; pedicels 1–7 mm long; peduncle, axes, bracts, and pedicels glabrous or sparsely to densely pilosulous, green to yellow; *flowers* distylous, with hypanthium glabrous, ellipsoid, 1.2–1.5 mm long; *calyx* limb glabrous, 1–1.5 mm long, divided nearly to base, lobes triangular to deltoid, acute to obtuse, entire; *corolla* tubular-funnelform, yellow, a little swollen at base, straight there and in tube, externally glabrous, internally glabrous except for a pilose ring ca. 2 mm wide at ca. 2 mm above base, tube 16–17 mm long, 4–6 mm diam. near middle, lobes triangular, ca. 3 mm long, acute, not much thickened adaxially, in bud with sinuses at base prolonged into wings 0.3–1.5 mm long; *anthers* in short-styled form ca. 4 mm long, partially exserted, in long-styled form ca. 3 mm long, positioned ca. ⅔ of length of tube above base; *stigmas* in short-styled form ca. 4 mm long, positioned ca. ⅔ of length of tube above base, in long-styled form ca. 1 mm long, exserted; *disk* ca. 1 mm high. *Infructescences* and *fruit* not seen. Wet forest at 1650–2600 m, southeastern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its stipules with truncate continuous sheaths and short broad lobes, pyramidal inflorescences, and tubular-funnelform yellow corollas with the sinuses in bud shortly to well expanded into short wings. The specific epithet refers to the yellow color of the flowers. This new species is similar to *Palicourea thyrsiflora*, which has usually narrower and longer stipule lobes, inflorescence branches yellow to usually red or orange, and corollas usually tubular and yellow becoming orange or red with age, with the sinuses between the lobes sometimes a little saccate but not developed into wings, and the buds generally truncate rather than rounded on the top.

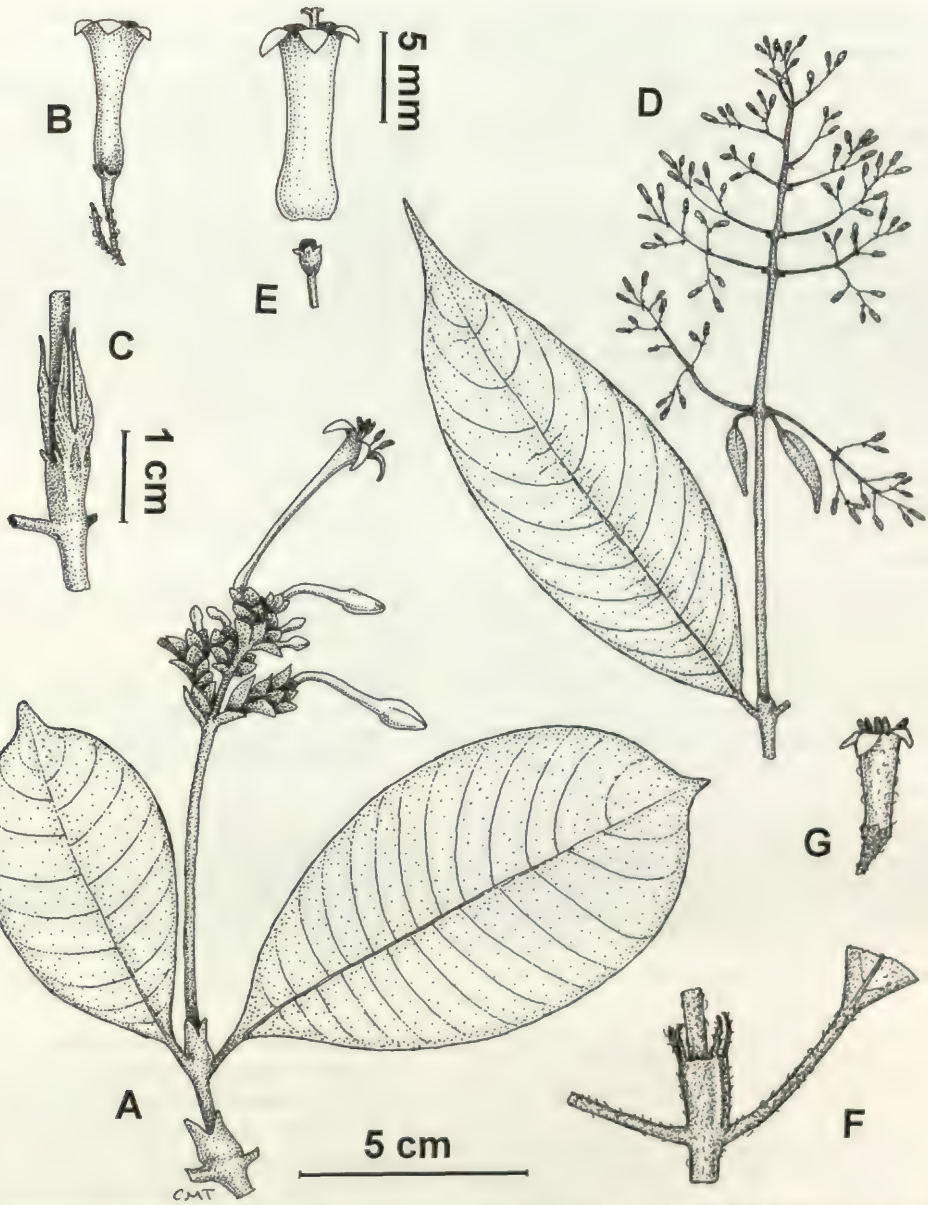

Figure 6. —A. *Palicourea candida*, flowering branch, based on *Molau & Eriksen 2149*. B, C, *Palicourea vulcanalis*, based on *Ownbey 2699*.—B. Flower.—C. Stipule. D, E, *Palicourea luteonivea*.—D. Flowering branch, based on *Zaruma 776*.—E. Calyx and corolla, partially dissected, based on *Neill et al. 7401*. F, G, *Palicourea prodiga*.—F. Stipule, based on *Holm-Nielsen et al. 27163*.—G. Flower, based on *Holm-Nielsen et al. 27250*. A, D, F to 5-cm scale; C to 1-cm scale; B, E, G to 5-mm scale.

Paratypes. ECUADOR. **Loja**: Nudo de Sabanilla, W slope on road to Yangana, *Harling & Andersson 21713* (GB, MO); Nudo de Sabanilla, W slope on road to Yangana-Valladolid, *Harling & Andersson 21825* (GB, MO). **Zamora-Chinchipe**: Nudo de Sabanilla-Valladolid, horse trail to Caserío Quebrada Honda, *Harling & Ståhl 26313* (GB), *Harling 27166* (GB); Romerillo, trail at limit of Parque Nacional Podocarpus, 04°13′S, 78°56′W, *Madsen & Bloch 75879* (AAU).

Palicourea candida C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: E upper slopes of Cordillera de Guacamayos, 11–13 km S of Cosanga on the Baeza-Tena road, 00°40′S, 77°52′W,

2100–2200 m, 22 Dec. 1987, *U. Molau & B. Eriksen 2149* (holotype, GB; isotype, AAU). Figure 6A.

Haec species a *Palicourea andrei* corolla et limbo calycino elongatis distinguitur.

Flowering at 2 m tall, to 15 m tall; stems somewhat succulent, glabrous. *Leaves* paired; *blades* elliptic to somewhat obovate, 8–18 × 4–10 cm, at apex acuminate with deltoid tips 3–5 mm long, at base cuneate to somewhat obtuse, papyraceous, adaxially glabrous or costa often puberulous, abaxially apparently paler, sparsely to moderately appressed-puberulous, more densely so on costa and secondary veins; secondary veins 12–16 pairs, generally extending to unite with margins, usually with 1 well-developed and often 2–3 weak intersecondary veins present between pairs of secondary veins, adaxially costa plane to prominulous and remaining venation plane, abaxially costa prominent, secondary veins plane to prominulous, and reticulated minor venation inconspicuous, plane to a little thickened; margins ciliolate; *petioles* glabrous, 5–25 mm long; *stipules* glabrous, laminar, ovate in outline, 12–18 mm long, overlapping laterally, bilobed for ca. ½, lobes ligulate to triangular, obtuse to rounded, ciliolate, with sinus acute to narrowly concave. *Inflorescences* apparently erect; peduncles 3–7.5 cm long; panicles pyramidal, 3–3.5 × 3.5–5 cm excluding corollas, with secondary axes 1–2(3) pairs, with flowers sessile in glomerules of 2–4; bracts entire, glabrous, acute to obtuse, those subtending secondary axes 8–15 mm long, lanceolate to oblanceolate, those subtending glomerules and individual flowers 3–7 mm long, lanceolate to ovate or suborbicular; peduncle, axes, and bracts puberulous, apparently green; *flowers* with hypanthium turbinate, 1–3 mm long, glabrescent to puberulous; *calyx* limb glabrous, 4–6 mm long, divided nearly to base, lobes elliptic, overlapping laterally, obtuse to rounded, entire to minutely ciliolate; *corolla* salverform to narrowly funnelform, white, a little swollen at base, generally straight there and perhaps also in tube, externally sparsely to moderately puberulous, internally glabrous except for a pilosulous to villosulous zone ca. 18 mm long in upper part of tube and ending below stamen attachment, tube 32–42 mm long, 2–2.5 mm diam. near middle, lobes narrowly triangular to ligulate, 8–9 mm long, acute; *anthers* in apparent short-styled form exserted, ca. 7 mm long; *stigmas* in apparent short-styled form positioned ca. ⅔ of length of tube above base, ca. 3 mm long; *disk* not seen. *Inflorescences* and *fruits* not seen. Wet forest at 1700–2200 m, east-central Ecuador. [Subg. *Montanae*, Sect. *Psychotrioides*, Ser. 9.]

This species is distinguished by its relatively large, laminar, bilobed stipules, flowers sessile in glomerules, relatively long calyx limb, and relatively long slender white corollas with a rather long pubescent portion internally. The species epithet refers to the white color of the corollas. The flowers appear to be adapted for pollination by nocturnal visitors such as hawkmoths, based on their white color and relatively long tubes. *Palicourea candida* is similar to *P. andrei*, which has sweetly fragrant flowers, calyx limbs 1–2 mm long, and corollas with tubes 20–25 mm long and lobes 6–8 mm long. The corolla tube appears to elongate markedly shortly before anthesis.

Paratypes. ECUADOR. **Napo**: Baeza-Tena road, southern slope of Cordillera de Guacamayos above Jondachi, *Harling & Andersson 16364* (GB). **Pastaza**: Colonia Alvarez Miño, ca. 6 km from Mera, *Lugo 828* (GB). **Tungurahua**: Cashurco, near Río Negro, northern side of Río Pastaza, *Lugo 800* (GB).

Palicourea chignul C. M. Taylor, sp. nov. TYPE: Ecuador. Carchi: Maldonado, Parroquia Tobar Donoso, Reserva Etnica Awá, Sabalera, 00°55′N, 78°32′W, 900 m, 22 Nov. 1992, *C. Aulestia, E. Aulestia & M. Guanga 852* (holotype, MO-4990807; isotype, QCNE not seen). Figure 7A.

Haec species a congeneris stipularum laminarium lobulis acutis, inflorescentia brevipedunculata pedicellis satis longis ac bracteis sat grandibus latisque praedita, lobulis limbi calycini satis bene evoluti lobulis lateraliter imbricatis, corolla sat longa atque fructu obovoideo distinguitur.

Flowering at 2 m tall, to 5 m tall; stems glabrous. *Leaves* paired; *blades* elliptic to broadly so or elliptic-oblong to somewhat oblanceolate, 14–29.5 × 7–18 cm, at apex shortly acuminate with deltoid to triangular tips 3–8 mm long, at base cuneate to obtuse, papyraceous, glabrous throughout or puberulous abaxially along costa; secondary veins 10–19 pairs, often looping to interconnect, without or usually with 1–2 weak intersecondary veins present between pairs of secondary veins, adaxially costa prominulous, secondary veins plane to prominulous, and minor venation plane, abaxially costa and secondary veins prominulous and minor venation plane to thickened; margins entire, thinly cartilaginous; *petioles* glabrous, 1.5–6.5 cm long; *stipules* glabrous or pubescent to minutely sericeous especially on distal parts, laminar, ovate in outline, 6–12 mm long, bilobed for ca. ½, lobes triangular, acute, entire, with sinus acute to concave and obtuse. *Inflorescences* generally erect; peduncles 0.5–

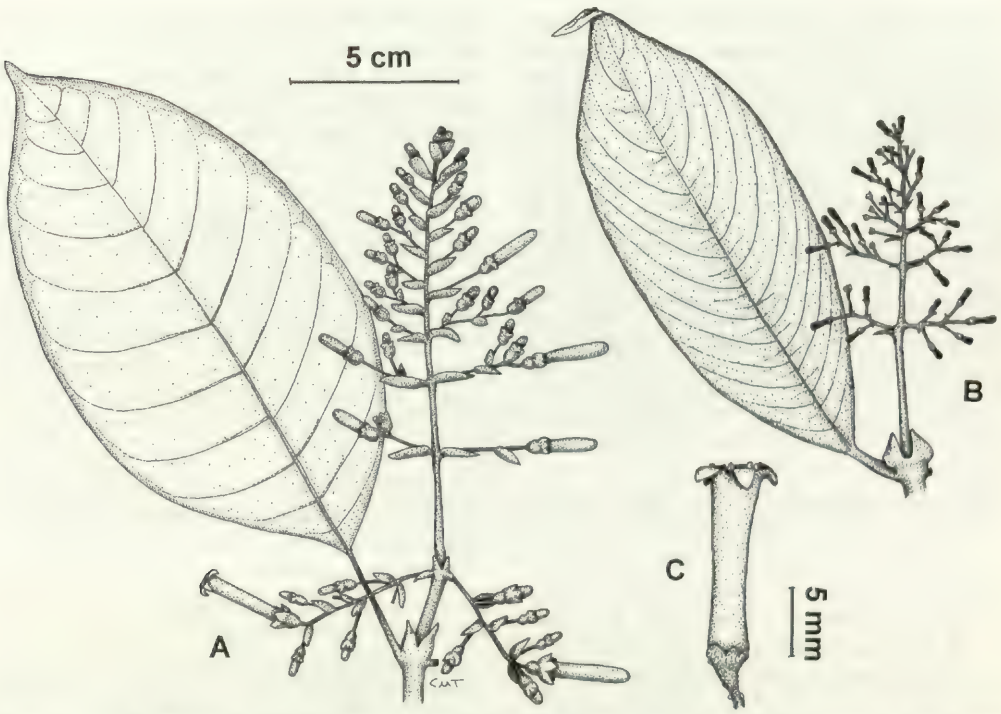

Figure 7. —A. *Palicourea chignul*, flowering branch, based on *Hoover et al. 2494*. B, C, *Palicourea deviae*, based on *Løjnant 12337*.—B. Flowering branch.—C. Flower. A, B to 5-cm scale.

2 cm long; panicles pyramidal to narrowly so, 5–14 × 5–7 cm excluding corollas, with secondary axes 5–10 pairs, the basalmost pair often strongly reflexed, with flowers pedicellate in cymules of 3–7; bracts ovate to lanceolate, elliptic or oblanceolate to ligulate, acute to obtuse or rounded, entire, those subtending secondary axes 6–15 mm long, those subtending pedicels 4–10 mm long; pedicels 4–14 mm long; peduncle, axes, bracts, and pedicels glabrous to puberulous, orange, red-orange, purple, or pink; *flowers* with hypanthium glabrous, turbinate to usually cupuliform, 2.5–4 mm long; *calyx* limb glabrous, pink, orange, or purple, 3–5 mm long, divided nearly to completely to base, lobes subequal to somewhat unequal on an individual flower, elliptic to suborbicular, reticulate-nerved, usually overlapping laterally, entire, obtuse to rounded; *corolla* tubular, orange to red or yellow, often grading in color along its length, swollen and a little gibbous at base, generally straight there and in tube, externally glabrous to usually minutely puberulous, internally glabrous except pilosulous in a ring ca. 1.5 mm wide at ca. ⅓ of length of tube above base, tube 20–25 mm long, ca. 2 mm diam. near middle, lobes triangular, ca. 2 mm long, acute; *disk* shorter than calyx. *Infructescences* similar to inflorescences except purple to rose; *fruit* obovoid, somewhat laterally flattened, 8–10 × 6–7 mm, glabrous, rose perhaps becoming black; *pyrenes* with 3–5 rather sharp longitudinal ridges. Wet forest at 900–1450 m, northwestern Ecuador to adjacent Colombia. [Subg. *Montanae*, Sect. *Obovoideae*, Ser. 6.]

This species is distinguished by its laminar stipules with acute lobes, shortly pedunculate inflorescences with relatively long pedicels and relatively large and broad bracts, well-developed calyx limb with laterally overlapping lobes, relatively long corolla, obovoid fruits, pyrenes with sharp longitudinal ridges, and combination of orange to purple or pink inflorescences with red to yellow corollas. It is similar to *Palicourea hospitalis*, which has longer inflorescences and shorter calyx limbs. The specific epithet is reported by several collectors to be the vernacular local name for this species.

One collection, *Drew & Wiggins 41* (F), is provisionally referred here, though the material is inadequate for conclusive identification. It conforms to the characters of this species except that it was collected in Imbabura Province, Ecuador, and it has secondary inflorescence axes, pedicels, and calyx limbs that are sparsely to moderately hirtellous and corollas that are densely pubescent externally

with multicellular stout trichomes 0.1–0.2 mm long. No mature corollas are present on this collection, which may represent another population of *Palicourea chignul* with a different pubescence pattern, or an undescribed related species.

Paratypes. COLOMBIA. **Nariño**: Altaquer, margen derecha de la carretera hacia Tumaco, *G. López-J. 253* (PSO). ECUADOR. **Carchi**: cantón Tulcán, parroquia Chical, Reserva Etnica Awá, centro Gualpí Medio, 01°02′N, 78°16′W, *Aulestia & Grijalva 1152* (MO), *Tipaz et al. 1972* (MO); trail from Pailón to Gualpí Chico area of Awá Reservation, 00°51′N, 78°16′W, *Hoover et al. 2394* (MO), *2419* (MO); Gualpí Chico area, 00°58′N, 78°16′W, *Hoover et al. 2494* (MO), *2778* (MO), *2781* (MO), *3392* (MO); plateau above San Marcos de los Coaiqueres, on trail toward Gualpí Bajo, 01°06′N, 78°17′W, *Øllgaard et al. 57365* (AAU), *57445* (AAU); near Maldonado, *van der Werff & Gudiño 10714* (MO).

Palicourea condorica C. M. Taylor, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: cantón Nangaritza, río Nangaritza, Pachicutza, faldas inferiores de la Cordillera del Cóndor, 04°07′S, 78°37′W, 5 Dec. 1990, *W. Palacios & D. Neill 6556* (holotype, MO-4990806; isotype, QCNE not seen). Figure 8D, E.

Haec species a congeneris foliis sat amplis, stipularum bilobarum sat grandium lobulis lanceolatis, inflorescentia subsessili ex pyramidali rotundata, limbo calycino brevi atque corolla lutea tubulari distinguitur.

Flowering at 3 m tall, to 5 m tall; stems apparently somewhat succulent, glabrous to puberulous or hirtellous often becoming glabrescent with age. *Leaves* paired; *blades* elliptic to broadly so, 8.5–36(50) × 5.5–18(26) cm, at apex acuminate with deltoid tips 3–10 mm long, at base cuneate to obtuse and sometimes attenuate, papyraceous to chartaceous, adaxially glabrous, abaxially puberulous, more densely so on costa and secondary veins; secondary veins 9–17 pairs, usually extending to unite with margins or occasionally looping to interconnect in most distal part of blade, without or sometimes with 1(2) weak intersecondary veins present between pairs of secondary veins, adaxially costa prominulous and canaliculate and secondary veins and reticulated minor venation plane to slightly thickened, abaxially costa prominent, secondary veins thinly prominulous, and minor venation plane to thickened; margins thinly cartilaginous; *petioles* 2–9(14) cm long, puberulous; *stipules* moderately to densely puberulous, united around the stem in a continuous truncate sheath 2–4 mm long, lobes lanceolate to ovate, 15–20 mm long, acute, rounded laterally, margins entire, with sinus concave to truncate. *Inflorescences* erect, subsessile; panicles pyramidal, 6(20) × 9(22) cm excluding corollas, with secondary axes 3–5 pairs, the basal pair relatively long and usually reflexed, with flowers pedicellate in cymules of 3–7; bracts subtending secondary axes triangular to lanceolate, 5–12 mm long, acute, those subtending pedicels 0.5–1 mm long, triangular, acute; pedicels 2–6 mm long; axes, branches, bracts, and pedicels glabrous or sparsely to moderately hirtellous, yellow to red-orange; *flowers* distylous, with hypanthium turbinate to cylindrical, 1–1.5 mm long, glabrous; *calyx* limb glabrous, 0.5–1 mm long, divided nearly to completely to base, lobes triangular, entire, subequal, acute; *corolla* tubular, yellow, a little swollen at base, generally straight there and in tube, externally glabrous, internally glabrous except for a pilose ring 1–1.5 mm wide at ca. 2 mm above the base, tube ca. 12 mm long, ca. 3 mm diam. near middle, lobes triangular, 2–4 mm long, acute, adaxially thickened and hooked, abaxially thickened to usually somewhat appendaged, appendages to 0.5 mm long; *anthers* in long-styled form ca. 4 mm long, positioned at ca. ⅓ of length of tube above base, in short-styled form not seen in good condition; *stigmas* in long-styled form exserted, not seen in good condition, in short-styled form ca. 4 mm long, positioned ca. ⅔ of length of tube above base; *disk* ca. 1 mm high. *Infructescences* and *fruit* not seen. Wet premontane forest at 900–1700 m, southern Ecuador. [Subg. *Montanae*, Sect. *Cephaeloides*, Ser. 11.]

This species is distinguished by its relatively large leaves, relatively large stipules with lanceolate lobes, subsessile pyramidal to rounded inflorescences, relatively short calyx limb, and tubular yellow corollas. It is similar to *Palicourea harlingii*, which has rounded-corymbiform inflorescences and calyx limbs 1.5–2 mm long; and to *P. macbridei* of Peru, which has purple flowers and calyx limbs 2–3 mm long with the lobes unequal on an individual flower. The specific epithet refers to the Cordillera del Cóndor, in the border region of Ecuador and Peru, where the type specimen was collected.

Paratypes. ECUADOR. **Morona-Santiago**: banks of the Río Ontza, Cordillera Cutucú, 02°40′S, 78°W, *Camp 1182* (S); cantón Gualaquiza, Cordillera del Cóndor, Cuangos, 20 km E of Gualaquiza, 03°29′S, 78°14′W, *Gentry 80116* (MO); Plan del Milagro at cross-road between Limón and Indanza, *Harling & Andersson 24522* (GB, MO); along new road Méndez-Morona, Km 30–35, *van der Werff & Gudiño 11261* (MO). **Zamora-Chinchipe**: cantón Nangaritza, Pachicutza, camino al Hito, 04°07′S, 78°37′W, *Palacios et al. 8287* (MO).

Palicourea corniculata C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: Baeza-Tena road, Cosanga, 4 Feb. 1980, *G. Harling & L. Andersson 16227* (holotype, GB; isotype, MO-4278911). Figure 9C, D, E.

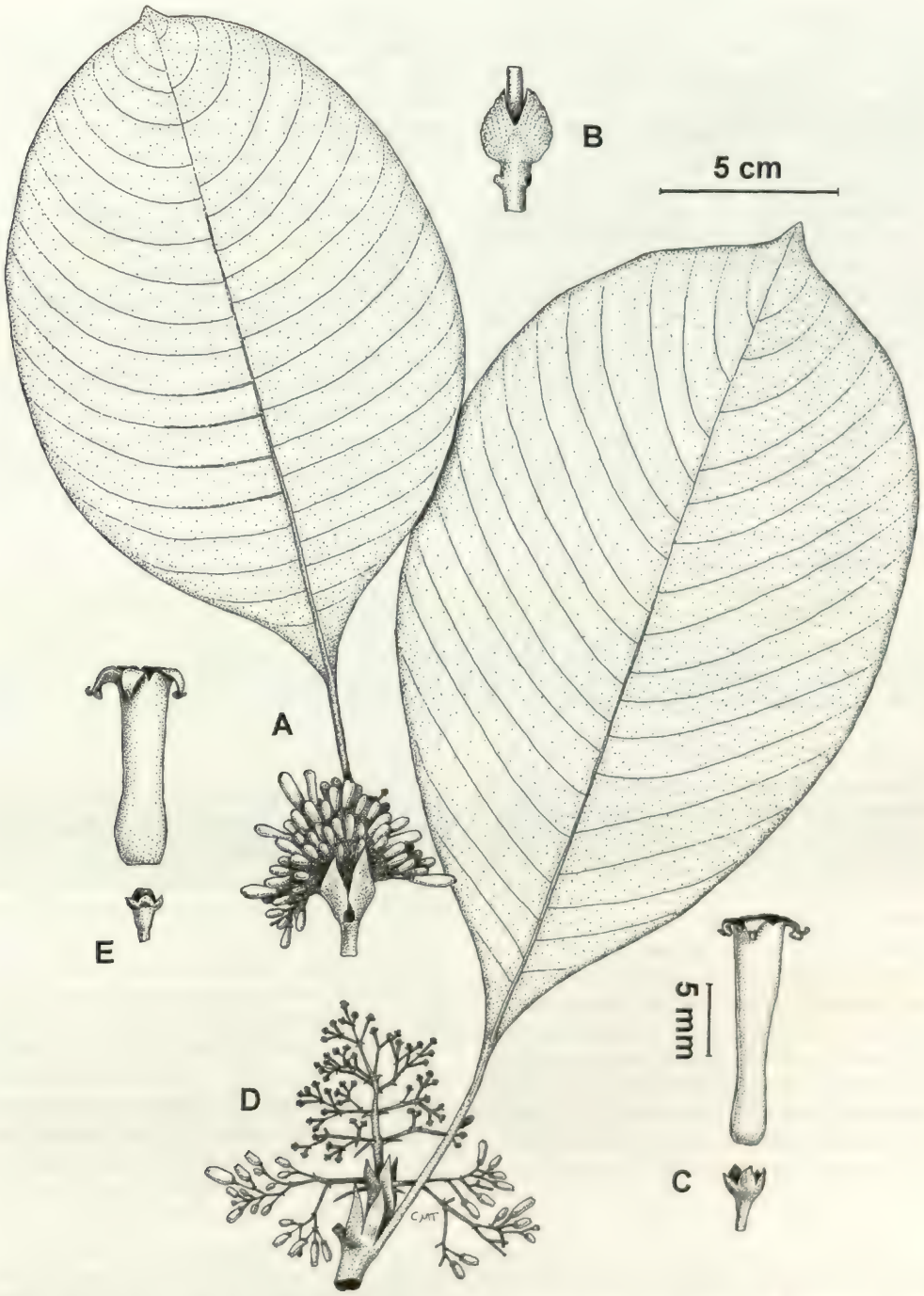

Figure 8. A–C, *Palicourea harlingii*, based on *Harling & Andersson 16917*.—A. Habit.—B. Stipule.—C. Flower, partially dissected. D, E, *Palicourea condorica*, based on *Palacios et al. 8287*.—D. Habit.—E. Flower, partially dissected. A, B, D to 5-cm scale; C, E to 5-mm scale.

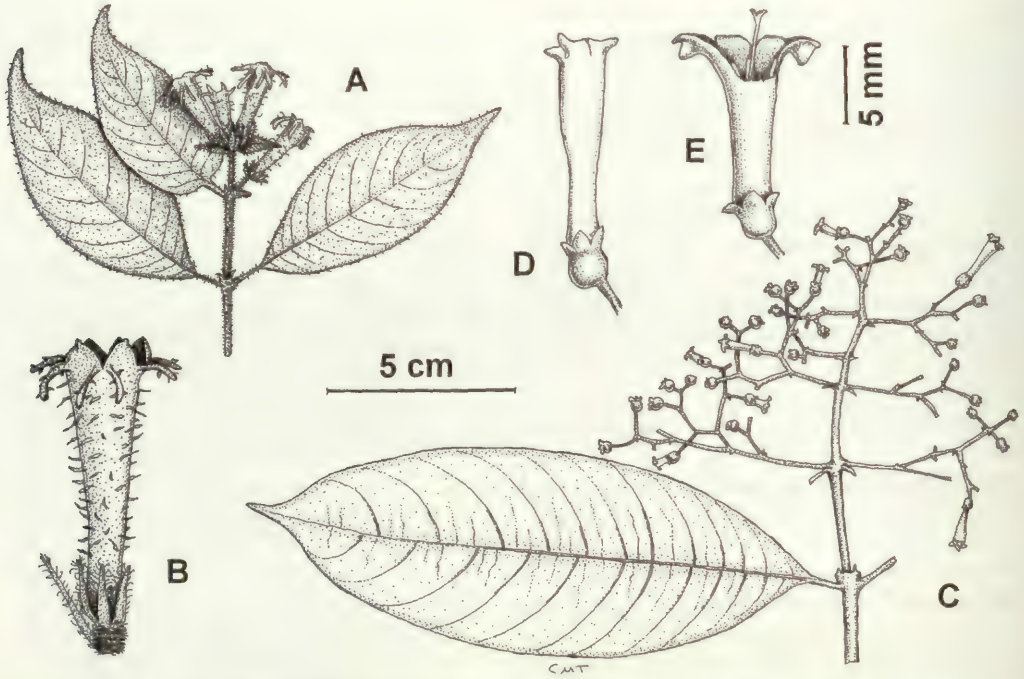

Figure 9. A, B, *Palicourea cornigera*, based on *Harling & Ståhl 26319*.—A. Flowering branch.—B. Flower. C–E, *Palicourea corniculata*, based on *Balslev & Madsen 10339*.—C. Flowering branch.—D. Flower in bud.—E. Flower, partially dissected. A, C to 5-cm scale; B, D, E to 5-mm scale.

Haec species a congeneris stipulis truncatis vaginantibus, hypanthio ex hemisphaerico ovoideo subglobosove diametro 2–3 mm atque corolla ex tubulari subinfundibuliformi typice inferne azurea et superne flava lobulos appendicibus bene evolutis praeditos habente distinguitur.

Flowering at (0.6)2 m tall, to 8 m tall; stems glabrous. *Leaves* paired; *blades* elliptic, 6.5–20 × 2–7 cm, at apex acute to usually acuminate with tips 5–10 mm long and deltoid, at base acute to cuneate, chartaceous, glabrous throughout or often sparsely to moderately hirsute along costa on abaxial surface; secondary veins 8–16 pairs, usually extending at least weakly to margins in basal part and looping to interconnect in distal part, with 1–2(3) intersecondary veins usually present between pairs of secondary veins, adaxially costa slenderly prominulous and remaining venation plane, abaxially costa prominulous, secondary veins thickened to prominulous, and reticulated minor venation plane to sometimes a little thickened; margins thinly cartilaginous; *petioles* glabrous, 0.8–2 cm long; *stipules* glabrous, united around the stem in a continuous truncate sheath 3–5 mm long, lobes deltoid to narrowly triangular, 1–2 mm long, acute to obtuse, entire. *Inflorescences* erect; peduncles 1–3 cm long; panicles pyramidal, 6.5–13 × 9–12.5 cm excluding corollas, with secondary axes 4–8 pairs, with flowers pedicellate in lax cymules of 3–7; bracts lanceolate to ovate or triangular, acute, entire to ciliolate, those subtending secondary axes 3–6 mm long, those subtending pedicels or borne along their length 0.5–2 mm long; pedicels 2–7 mm long; peduncle, axes, bracts, and pedicels red to violet or purple, glabrous; *flowers* distylous, with hypanthium hemispherical to ovoid or subglobose, glabrous, green to yellow, 2–3 mm diam., usually with pedicel attached obliquely; *calyx* limb glabrous, green to yellow, 1–1.5(2) mm long, divided partially to completely to base, lobes ligulate, subequal to somewhat unequal on an individual flower, obtuse to rounded, entire to ciliolate; *corolla* tubular to somewhat funnelform, yellow, rarely white, or usually blue to violet in tube and yellow on lobes and sometimes also upper part of tube, somewhat swollen at base, straight to bent there, generally straight in tube, externally glabrous, internally glabrous except for a densely pilose ring ca. 1.5 mm wide at ca. ⅓ length of tube above base, tube 10–15 mm long, 2.5–4 mm diam. near middle, lobes triangular to somewhat deltoid, 2.5–3 mm long, acute, at apex with abaxial, carnose, deltoid appendage 1.5–2.5 mm long; *anthers* in long-styled form ca. 2 mm long, included, in short-styled form ca. 4 mm

long, partially exserted; *stigmas* in long-styled form ca. 0.8 mm long, well exserted, in short-styled form ca. 2.5 mm long, positioned just below anthers; *disk* ca. 1 mm high. *Infructescences* similar to inflorescences; *fruit* subglobose, 5–7 mm diam.; *pyrenes* with low, rather sharp longitudinal ridges. Wet forest at 1800–2600 m, eastern slopes of Andean Cordillera in northern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its stipules with truncate sheaths and short lobes, pyramidal inflorescences, hypanthia hemispherical to ovoid or subglobose and relatively large, and tubular to somewhat funnelform corollas that are typically blue in the lower part and yellow in the upper and have lobes with well-developed appendages. The specific epithet refers to these appendages, which develop on the young flower buds, giving them a distinctive profile.

Paratypes. ECUADOR. **Napo**: cantón Quijos, Sierra Azul (Agrícola Industrial Río Aragón), campamento Estero Chico, 00°41′S, 77°56′W, *Alvarez et al. 530* (MO, QCNE), *547* (MO, QCNE); cantón Quijos, parroquia de Baeza, comunidad de Santa Lucía de Bermejo, 00°31′S, 77°55′W, *Alvarez et al. 855* (MO, QCNE), *1017* (MO, QCNE); Cordillera Guacamayo, *Asplund 8824* (S); Cosanga, *Asplund 9565* (S); road Baeza-Napo, Cosanga, 20 km S of Baeza, 00°37′S, 77°52′W, *Balslev & Madsen 10339* (AAU, MO); Baeza-Tena road on southern slopes of Cordillera de Guacamayos, *Harling & Andersson 16415* (GB); slopes of Guagra Urcu, on the loma above Río Bretania, 00°28′S, 77°45′W, *Holm-Nielsen et al. 26779* (AAU), *26887* (AAU); parroquia Cosanga, entre el río Aliso y el río Cosanga, *Jaramillo et al. 12048* (GB); parroquia Cosanga, a 6 km de la carretera Cosanga-El Aliso, *Jaramillo et al. 12107* (GB); vía Baeza-Cotundo, *Little & Campuzano 158* (MO); along Cosanga River at Cosanga, S of Baeza on trail to Tena, *Ownbey 2693* (MO); cantón Quijos, Cosanga, entre el río Vinilla y el río Cosanga, 00°34′S, 77°52′W, *Palacios et al. 9590* (MO, QCNE); road Baeza-Tena, road leading W 2 km N of Cosanga, 00°33′S, 77°53′W, *Persson et al. 3* (GB).

Palicourea cornigera C. M. Taylor, sp. nov. TYPE: Ecuador. Zamora-Chinchipe: above Valladolid on road to Yangana, 2700 m, 2 Feb. 1985, *G. Harling & L. Andersson 21465* (holotype, MO-4278930; isotype, GB). Figure 9A, B.

Haec species a congeneris corolla trichomatibus azureis 1–3 mm longis externe vestita ac sinibus lobulorum ad margines appendicibus corniformibus bene evolutis praeditis distinguenda.

Flowering at 0.5 m tall, to 2 m tall; stems occasionally clambering, densely pilosulous or hirtellous to hirsute. *Leaves* paired; *blades* elliptic, 4–15.5 × 1.4–4.5 cm, at apex acute to usually acuminate with tips slender, sometimes falcate, 1–1.5 cm long, at base acute to cuneate or obtuse, membranaceous to papyraceous, adaxially sparsely to moderately pilosulous or hirtellous except densely so on costa, abaxially densely pilosulous to hirtellous; secondary veins 9–17 pairs, frequently extending to unite with margins, usually with 1–2 weak intersecondary veins present between pairs of secondary veins, adaxially venation plane, abaxially costa prominulous, secondary veins plane or usually a little thickened, and minor venation plane; margins thinly cartilaginous, entire to ciliolate; *petioles* moderately to densely hirtellous or pilosulous to hirsute, 3–12 mm long; *stipules* moderately to densely pilosulous or hirtellous, united around the stem in a continuous truncate sheath 2.5–3 mm long, lobes linear, 2–5 mm long, spreading-pilose to hirsute. *Inflorescences* perhaps nodding, sometimes tripartite and apparently sessile; peduncles 1–3 cm long; panicles subcapitate or branched once, 1–2 × 2–2.5 cm excluding corollas, with flowers sessile to subsessile in glomerules of 3–5, bracts linear, those subtending glomerules 7–9 mm long, those subtending flowers 3–8 mm long; peduncle, axes, and bracts densely hirtellous to hirsute with blue to purple trichomes; *flowers* distylous, with hypanthium ca. 1 mm long, turbinate, densely pilose with linear blue trichomes 1–3 mm long; *calyx* limb green, 3.5–6 mm long, divided nearly to base, lobes narrowly lanceolate, unequal by ca. 25% or so on an individual flower, acute to acuminate, glabrous to moderately pubescent with blue linear trichomes 1–3 mm long; *corolla* funnelform, white to blue or sometimes yellow distally, a little swollen and gibbous at base, generally straight there and in tube, externally moderately to densely pubescent with linear blue trichomes 1–3 mm long, internally glabrous except for a densely pilose ring ca. ⅓ of length of tube above the base, tube 15–20 mm long, 3.5–5 mm diam. near middle, lobes deltoid, 2–2.5 mm long, slightly thickened at apex adaxially, with 2 linear pubescent appendages 3–5 mm long near base, one on each side; *anthers* in short-styled form ca. 3 mm long, partially exserted, in long-styled form ca. 2 mm long, positioned ca. ⅔ of length of tube above base; *stigmas* in long-styled form 0.5–1 mm long, exserted, in short-styled form ca. 3 mm long, positioned near or just above tube middle; *disk* not seen. *Infructescences* and *fruit* not seen. Wet forest at 1700–2700 m, southern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 4, Subser. f.]

This species is distinguished by its corollas that are externally pubescent with blue trichomes 1–3 mm long and bear two well developed horn-like appendages from the base on each side of the ab-

axial part of the lobes, hirtellous or pilosulous pubescence throughout, linear stipule lobes and bracts, sessile or subsessile flowers borne in one or a few glomerules, and well-developed calyx limb with narrow lobes. The paired appendages attached near the base on each side of each corolla lobe are unique in the genus and perhaps the family. The specific epithet refers to these appendages. When the flower is in bud, these appendages are spreading and can be mistaken for narrow corolla lobes, but the corolla lobes are broad and much shorter. *Palicourea cornigera* is similar in aspect to *P. calycina*, which lacks corolla lobe appendages.

Paratypes. ECUADOR. **Loja**: Nudo de Sabanilla, north part, *Harling et al. 20520* (GB, MO). **Morona-Santiago**: road General Proaño-Aschlí, Km 22, 02°15′S, 78°13′W, *Persson et al. 34* (GB, MO). **Zamora-Chinchipe**: Loja-Zamora road, E of pass, *Harling & Andersson 22108* (GB, MO); along road Valladolid-Nudo de Sabanilla, *Harling & Madsen 25255* (GB); Nudo de Sabanilla-Valladolid, horse trail to Caserío Quebrada Honda, *Harling & Ståhl 26319* (AAU, GB).

Palicourea deviae C. M. Taylor, sp. nov. TYPE: Ecuador. Sucumbíos: Cartagena, Km 25 from El Carmelo on road towards La Bonita, 00°37′N, 77°30′W, 13 Apr. 1979, *B. Løjtnant, U. Molau & M. Madison 12337* (holotype, AAU; isotype, GB). Figure 7B, C.

Haec species a congeneris lobulis stipularibus lanceolatis asymmetricis bene evolutis, limbo calycino 1.5–1.8 mm longo atque corolla ex azurea purpurea distinguitur.

Flowering at 3 m tall; stems moderately to densely hirsutulous becoming glabrescent with age. *Leaves* paired; *blades* elliptic to oblanceolate, 7–17 × 2.5–5.8 cm, at apex acuminate with tips 1–2 cm long, at base cuneate to obtuse, chartaceous to subcoriaceous, adaxially glabrous except hirtellous along costa, abaxially moderately to densely hirtellous throughout; secondary veins 13–14 pairs, usually extending to unite with margins at least in distal part, with 1(3) weak intersecondary veins usually present between pairs of secondary veins, adaxially with costa plane to slightly sulcate and secondary veins and reticulated minor venation impressed, abaxially with costa prominent, secondary veins prominent to prominulous, and minor venation prominulous to thickened; margins thinly cartilaginous, often somewhat revolute; *petioles* moderately to densely hirsutulous, 0.8–2 cm long; *stipules* moderately to densely hirsutulous or puberulous, united around the stem in a continuous sheath 5–7 mm long, with interpetiolar free portion 5–14 mm long, divided for ca. ½ to completely, lobes lanceolate, laterally expanded to auriculate at base, 2.5–6 mm wide, acute, entire to slightly erose, with sinus acute to narrowly concave. *Inflorescences* erect to somewhat deflexed; peduncles 1.5–6.5 cm long; panicles pyramidal, 8–14 × 6–12 cm excluding corollas, with secondary axes 10–12 pairs, with flowers pedicellate in cymules of 3–7; bracts narrowly triangular, acute, those subtending secondary axes 4–11 mm long, those subtending pedicels 1.5–3 mm long; pedicels 1–6 mm long; peduncle, axes, bracts, and pedicels moderately to densely hirsutulous, purple to magenta; *flowers* with hypanthium 1–1.5 mm long, turbinate, moderately to densely pilosulous; *calyx* limb pilosulous, 1.5–1.8 mm long, divided nearly to completely to base, lobes lanceolate to elliptic or ovate, usually slightly unequal on an individual flower, obtuse to acute; *corolla* tubular, blue to purple, a little swollen and gibbous at base, generally straight there and in tube, externally glabrous or minutely puberulous on lobes, internally glabrous except for a pilose ring ca. 1 mm wide at ca. ¼ of length of tube above base, tube 13–14 mm long, ca. 3.5–4 mm diam. near middle, lobes deltoid, ca. 2 mm long, acute, adaxially and abaxially a little thickened at apex; *anthers* in short-styled form ca. 4 mm long, partially exserted; *stigmas* in short-styled form ca. 3 mm long, positioned just above middle of corolla tube; *disk* ca. 1 mm high. *Infructescences* similar to inflorescences; *fruit* subglobose to ellipsoid, ca. 5 × 4.5 mm, hirtellous; *pyrenes* with low rounded longitudinal ridges. Cloud forest at 2800 m, Ecuador and probably western Colombia. [Subg. *Montanae*, Sect. *Montanae*, Ser. 4, Subser. e.]

This species is distinguished by its well-developed stipules with a truncate continuous sheath and lanceolate, laterally expanded lobes, chartaceous to subcoriaceous leaves with the margins typically a little revolute, pyramidal purple inflorescences, calyx limb 1.5–1.8 mm long and divided nearly or completely to the base, tubular purple corollas, and subglobose to ellipsoid fruits. It is similar to *Palicourea toroi* of Colombia, which has calyx limbs 3.5–4 mm long; and to *P. stipularis*, which has narrowly triangular stipule lobes and calyx limbs 0.9–1.2 mm long. This handsome species is named in honor of botanist Wilson Devia of Tuluá, Colombia, who showed it to me in the Cordillera Central in Valle, Colombia, although only the one collection from Ecuador has been seen. In Colombia *P. deviae* flowers in the rainy season, when relatively fewer collections have been made, which may explain in part why it is so poorly represented in herbaria.

Palicourea gentryi C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: 17 km W of Lumbaque [sic; Lumbaqui] (70 km W of Lago Agrio), 1130 m,

4 Nov. 1974, *A. Gentry 12437* (holotype, MO-2791014; isotypes, MO-2779141, MO-3131952). Figure 4F.

Haec species a *Palicourea* subalata inflorescentia minore congestioreque bracteas longiores gerente, hypanthio cupuliformi majore, limbi calycini lobulis subaequalibus atque corolla extus villosa distinguitur.

Flowering at 2 m tall, to 4 m tall; stems glabrous. *Leaves* paired; *blades* elliptic, 10–19 × 3.5–7.4 cm, at apex acute to usually acuminate with tips 8–18 mm long, at base acute to somewhat tapered, papyraceous, adaxially glabrous, abaxially sparsely to moderately hirtellous, more densely so on costa and secondary veins; secondary veins 11–18 pairs, generally extending weakly to unite with margins, without or with 1–2 weak intersecondary veins sometimes present between pairs of secondary veins, adaxially costa thinly prominulous and remaining venation plane to a little thickened, abaxially costa prominent, secondary veins prominulous, and reticulated minor venation plane; margins ciliolate; *petioles* glabrous, 5–30 mm long; *stipules* glabrous, united around the stem in a continuous truncate sheath 1.5–3 mm long, lobes narrowly triangular, 5–7.5 mm long, acute. *Inflorescences* perhaps erect, sometimes tripartite and appearing sessile; peduncles 2–5.5 cm long; panicles rounded-corymbiform, 1–3 × 2–7 cm excluding corollas, with secondary axes 1–3 pairs, with flowers pedicellate in cymules of 4–9; bracts subtending secondary axes elliptic to lanceolate, 6–10 mm long, acute, ciliolate, those subtending pedicels narrowly triangular to lanceolate, acute to acuminate, 1–4 mm long; pedicels 3–6 mm long; peduncle, axes, bracts, and pedicels glabrous, perhaps yellow; *flowers* with hypanthium cupuliform, glabrous, 1.5–2 mm long; *calyx* limb glabrous, 1–1.2 mm long, divided for ⅕–¼, lobes deltoid, entire; *corolla* tubular to somewhat funnelform, white to yellow, a little swollen at base, generally straight there and in tube, externally moderately to densely villous with linear multicellular trichomes ca. 1 mm long, internally glabrous except for a densely villous ring ca. 1 mm wide at ca. 4 mm above base, tube ca. 13 mm long, ca. 2 mm diam. near base, lobes triangular, ca. 3 mm long, acute, slightly thickened at apex; *anthers* in long-styled form ca. 2.5 mm long, positioned in upper ⅓ of tube; *stigmas* not seen; *disk* ca. 0.8 mm high. *Inflorescences* and *fruit* not seen. Wet forest at 800–1130 m, east-central Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is similar to *Palicourea subalata*, from which it can be distinguished by its smaller, more congested inflorescences with longer bracts, longer cupuliform hypanthium, calyx limb with lobes subequal on an individual flower, and corollas villous externally. This species is named in honor of American botanist Alwyn H. Gentry (1945–1993), whose work on the floristics and diversity of the Andean flora has contributed to our knowledge of many *Palicourea* species.

Paratype. ECUADOR. **Napo**: de la carretera entre Reventador y Lumbaqui, 10 km al sur, Río Tigre, 00°05′S, 77°24′W, *Neill 7532* (AAU).

Palicourea harlingii C. M. Taylor, sp. nov. TYPE: Ecuador. Pastaza: cantón Pastaza, along road between Mera and Río Anzu, which is 11.7 km N of main plaza in Mera, on Puyo-Baños road, 01°20′S, 78°06′W, 5 Apr. 1992, *T. B. Croat 73584* (holotype, MO-4990802). Figure 8A–C.

Haec species a *Palicourea condorica* stipulis laminaribus (non vaginantibus), inflorescentia rotundato-corymbiformi, bracteis floralibus longioribus atque limbo calycino 1.5–2 mm longo distinguitur.

Flowering at 2.2 m tall, to 5 m tall; stems glabrous. *Leaves* paired; *blades* elliptic to broadly so, 19–27.5 × 11–19 cm, at apex shortly acuminate with deltoid tips 5–10 mm long, at base cuneate to obtuse and sometimes attenuate, papyraceous, adaxially glabrous, abaxially puberulous especially on costa and secondary veins; secondary veins 16–18 pairs, generally extending to unite with margins, without or with 1–2 weak intersecondary veins present between pairs of secondary veins, adaxially costa prominulous and canaliculate and secondary veins and reticulated minor venation plane to slightly thickened, abaxially costa prominent, secondary veins thinly prominulous, and minor venation plane to thickened; margins thinly cartilaginous; *petioles* glabrous to puberulous, 5.5–11 cm long; *stipules* moderately to densely puberulous, laminar, ovate in outline, with undivided interpetiolar portion 3–5 mm long, lobes 20–25 mm long, lanceolate to ovate, rounded to subauriculate laterally, acute to acuminate, entire, with sinus concave to truncate. *Inflorescences* erect, subsessile; panicles rounded-corymbiform, rather congested, 3–5 × 4–6 cm excluding corollas, with secondary axes 2–3 pairs, with flowers pedicellate and sessile together in cymules of 3–5; bracts ciliolate, those subtending secondary axes 5–12 mm long, lanceolate to narrowly elliptic, acute, those subtending pedicels 3–5 mm long, lanceolate to oblanceolate, acute to obtuse; pedicels 0–5 mm long; axes, bracts, and pedicels glabrous, yellow; *flowers* with hypanthium 1.2–1.5 mm long, turbinate to cylindrical, glabrous; *calyx* limb glabrous, 1.5–2 mm

long, divided nearly or completely to base, lobes triangular to ovate, acute to acuminate, ciliolate; *corolla* tubular, yellow, somewhat swollen at base, generally straight there and in tube, externally glabrous, internally glabrous except for a pilose ring 1.5–2 mm long at ca. ⅓ of length of tube above base, tube ca. 16 mm long, ca. 3 mm diam. near middle, lobes 1.5–2 mm long, triangular, adaxially thickened and hooked, abaxially with appendages 0.5–1 mm long; anthers in long-styled form ca. 5 mm long, positioned ca. ¾ of length of tube above base; *stigmas* in long-styled form exserted, ca. 1 mm long; *disk* ca. 1 mm long. *Infructescences* and *fruit* not seen. Wet forest at 1200–1380 m, northeastern Ecuador. [Subg. *Montanae*, Sect. *Cephaeloides*, Ser. 11.]

This species is distinguished by its relatively large leaves, relatively long, bilobed, laminar stipules, subsessile corymbiform-rounded inflorescences, relatively well-developed floral bracts and calyx limb, and tubular yellow corollas with the lobes abaxially appendaged, especially in bud. It is similar to *Palicourea condorica*, which can be distinguished by its stipules with continuous truncate sheaths, pyramidal inflorescences, and shorter floral bracts, calyx limb, and abaxial thickenings on the corolla lobes. This handsome species is named in honor of Swedish botanist Gunnar Harling, whose extensive work has contributed significantly to our scientific knowledge of the Ecuadorian flora.

Paratype. ECUADOR. **Pastaza**: Colonia Játiva, ca. 7 km N of Mera, *Harling & Andersson 16917* (GB, MO).

Palicourea jaramilloi C. M. Taylor, sp. nov. TYPE: Ecuador. Loja: Loja-Saraguro Km 18, 03°54′08″S, 79°14′54″W, 21 Apr. 1994, *P. M. Jørgensen, C. Ulloa, H. Vargas & G. Abendaño 459* (holotype, MO-5006718; isotypes, LOJA not seen, QCA not seen, QCNE not seen). Figure 5F, G.

Haec species a *Palicourea azurea* corollae luteae tubo ca. 7 mm longo distinguitur.

Flowering at 1 m or perhaps less, to 2 m tall; stems weak to scrambling, densely hirtellous. *Leaves* paired; *blades* elliptic to rather narrowly so, 5–14.5 × 2–5.5 cm, at apex acute to usually acuminate with tips 3–8 mm long, at base cuneate to obtuse, subcoriaceous, adaxially nitid and glabrous or sparsely hirtellous along costa, abaxially moderately to densely hirtellous; secondary veins 8–13 pairs, extending to unite with margins or often looping to interconnect with each other and margin in a closely set reticulum, with 1–2(3) weak intersecondary veins usually present between pairs of secondary veins, adaxially costa thinly prominulous and secondary veins and reticulated minor venation plane to thickened, abaxially costa prominent, secondary veins prominulous, and minor venation thickened; margins cartilaginous, often rather thickly so, entire or ciliolate; *petioles* hirtellous, 5–15 mm long; *stipules* moderately to densely hirtellous, often becoming glabrescent and indurate with age, united around the stem in a continuous truncate sheath 4–6.5 mm long, strongly quadrate, usually somewhat costate on angles, lobes narrowly triangular, 5–8 mm long, acute, with sinus truncate. *Inflorescences* erect, often tripartite and apparently sessile; peduncles 2–4 cm long; panicles pyramidal, 6.5–14 × 5–12 cm excluding corollas, secondary axes 5–12 pairs, with flowers subsessile to shortly pedicellate together in cymules of 5–11; bracts narrowly triangular to deltoid or ovate, acute, those subtending secondary axes 3–8 mm long, those subtending pedicels 1–3 mm long; pedicels 0.5–4 mm long; peduncle, axes, bracts, and pedicels moderately to densely hirtellous, yellow or greenish yellow; *flowers* with hypanthium hirtellous, turbinate to cylindrical, 1–1.5 mm long; *calyx* limb hirtellous, 1–1.2 mm long, divided for ca. ½, lobes deltoid; *corolla* tubular to somewhat funnelform, yellow or greenish yellow to red, a little swollen at base, generally straight there, straight to curved in tube, externally moderately to densely hirtellous with trichomes to 0.5 mm long, in bud more densely so on lower part of tube, internally glabrous except for a villous ring ca. 1 mm wide at ca. ⅓ of length of tube above base, tube ca. 7 mm long, 1.5–2 mm diam. near middle, lobes deltoid, ca. 1.5 mm long, at apex somewhat thickened abaxially; *anthers* in short-styled form ca. 2 mm long, partially exserted; *stigmas* in short-styled form ca. 2 mm long, positioned at ca. ⅔ of length of tube above base; *disk* ca. 0.8 mm high. *Infructescences* similar to inflorescences; *fruit* ellipsoid, often somewhat flattened laterally, ca. 5 × 4 mm; *pyrenes* with 3–5 low rounded longitudinal ridges. Wet forest at 2600–3400 m, southern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 4, Subser. f.]

This species is distinguished by its dense hirtellous pubescence, stipules with truncate, continuous sheaths that are usually costate on the angles, subcoriaceous leaves, yellow inflorescences and flowers, rather long floral bracts, corollas with tubes ca. 7 mm long and hirtellous externally, and ellipsoid laterally flattened fruits. It is similar to *Palicourea azurea*, which has blue to purple corollas with tubes 15–16 mm long. The well-developed stipule sheaths with costate angles are similar to

those of *P. flavescens*. This species is named in honor of Ecuadorian botanist Jaime Jaramillo, who has collected extensively in Ecuador and contributed significantly to our knowledge of the flora of this country.

Paratypes. ECUADOR. **Loja**: carretera Loja-Zamora, desde el Km 16 al 24, *Jaramillo & Winnerskjold 5784* (AAU); Loja-Saraguro, Km 58, turnoff towards Fierro Urco, Km 1–2, 03°41′49″S, 79°16′22″W, *Jørgensen et al. 483* (MO); road Pichig-Fierro Urcu, Km 11 (ca. 15 Km SW of Saraguro), 03°41′S, 79°20′W, *Madsen 85448* (AAU); ca. 10 km SW of Loja, along road past University towards La Violeta, *van der Werff & Palacios 9074* (MO). **Zamora-Chinchipe**: road Loja-Zamora, Km 14, 04°S, 79°90′W, *Holm-Nielsen et al. 3959* (AAU, S).

Palicourea lugoana C. M. Taylor, sp. nov. TYPE: Ecuador. Pastaza: Mera, 4 Mar. 1940, *M. Lugo 14* (holotype, S). Figure 4E.

Haec species a congeneris folii costa prominente adaxialiter canaliculata, lobulis stipularibus ex obtusis rotundatis, limbo calycino 0.3–0.9 mm longo atque corolla flava valde gibbosa curvataque distinguitur.

Flowering at 1.3 m tall, to 6 m tall; stems glabrous. *Leaves* paired; *blades* elliptic to elliptic-oblong, 7.5–23 × 4–12 cm, at apex acute to shortly acuminate with deltoid tips 3–5 mm long, at base cuneate to obtuse, papyraceous, glabrous on both surfaces; secondary veins 9–17 pairs, spreading, broadly curved, usually extending to unite with margins at least in distal part of blade, with 1–2(3) intersecondary veins usually present between pairs of secondary veins, adaxially costa prominulous and narrowly to broadly canaliculate, secondary veins thinly prominulous, and minor venation reticulated and plane, abaxially costa prominulous to prominent, secondary veins plane to thickened, and minor venation plane; margins thinly cartilaginous, entire; *petioles* 1.5–3.5 cm long; *stipules* glabrous, laminar, ovate to ligulate in outline, laterally rounded and overlapping, 5–10 mm long, bilobed for ca. ⅓–½, lobes ligulate to triangular, obtuse to rounded, with sinus concave, minutely ciliolate. *Inflorescences* erect, sometimes tripartite and appearing sessile; peduncles 2.5–4.5 cm long; panicles pyramidal, 10.5–21 × 11–25 cm excluding corollas, with secondary axes 8–12 pairs, the basal pair typically 1.5–2 times as long as the next pair, with flowers pedicellate in cymules of 3–7; bracts narrowly triangular, acute, those subtending secondary axes 2–6 mm long, those subtending pedicels 1–2 mm long; pedicels (2)4–8 mm long; peduncle, axes, bracts, and pedicels moderately puberulous to short-pilosulous, yellow; *flowers* distylous, with hypanthium turbinate, slender, puberulous to glabrous, ca. 1 mm long; *calyx* limb glabrous to puberulous, 0.3–0.9 mm long, divided nearly to completely to base, lobes slightly to strongly unequal on an individual flower, lanceolate to triangular, acute to obtuse, entire; *corolla* funnelform, yellow, strongly gibbous and swollen at base, strongly constricted and bent to 90° just above this, generally straight in tube, externally glabrous, internally glabrous except for a narrow pilose ring at the constriction, tube 8–10 mm long, ca. 2 mm diam. near middle, lobes deltoid to triangular, 2–2.5 mm long, acute; *anthers* in long-styled form ca. 1.3 mm long, included, positioned in upper ⅓ of tube, in short-styled form partially exserted, ca. 1.3 mm long; *stigmas* in long-styled form ca. 0.8 mm long, exserted, in short-styled form ca. 1.5 mm long, positioned near middle of tube; *disk* ca. 0.8 mm long. *Infructescences* similar to inflorescences; *fruit* obovoid, somewhat flattened laterally, ca. 5 × 4.5 mm, glabrous; *pyrenes* with 3–5 low rounded longitudinal ridges. Wet forest at 1160–1380 m in central Ecuador, to 2000 m in northwestern Colombia. [Subg. *Montanae*, Sect. *Obovoideae*, Ser. 6.]

This species is distinguished by its leaves adaxially with secondary veins prominulous and costa prominulous to prominent and canaliculate, laminar stipules that are divided for ca. ⅓–½ of their interpetiolar length with lobes obtuse to rounded, pyramidal yellow inflorescences, calyx limb 0.3–0.9 mm long and lobed nearly or completely to base, corollas strongly gibbous at base and bent and constricted just above this, and obovoid fruits. It is similar to *Palicourea gibbosa*, which has stipules that are divided for ½ or more of their interpetiolar length and with acute lobes, leaves with generally longer and more slender tips and the costa not canaliculate adaxially, generally smaller inflorescences with shorter peduncles, and longer calyx limb; and to *P. asplundii*, which has calyx limbs 2–2.8 mm long. The specific epithet honors Ecuadorian plant collectors Manuel and Holguer Lugo, who have helped to document much of the Ecuadorian flora with excellent specimens.

Paratypes. COLOMBIA. **Antioquia**: municipio Frontino, region of Murrí, ca. 13 road-km from Nutibara, 06°40′N, 76°20′W, *McPherson 13368* (MO). ECUADOR. **Pastaza**: cantón Pastaza, along road between Puyo and Baños, ca. 3 km W of Mera at second bridge, *Croat 49714* (MO); along road between Mera and Río Anzu, 11.7 km N of main plaza in Mera, 01°20′W, 78°06′W, *Croat 73584* (MO); Mera, Mangayacu, *Harling 3189* (S); Mera, *Harling 3395* (S).

Palicourea luteonivea C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: Puerto Misahuallí, 8 km río abajo, margen derecha del río Napo, Reserva Florística Jatún Sacha, 01°04′S,

77°36′W, 2 Oct. 1986, *J. Zaruma 776* (holotype, MO-3596709; isotypes, AAU, GB, QAME). Figure 6D, E.

Haec species a *Palicourea thyrsiflora* inflorescentiae ramis luteis atque corolla alba distinguitur.

Flowering at 3 m tall, to 6 m tall; stems glabrous. *Leaves* paired; *blades* elliptic to elliptic-oblong, 10–22 × 2.5–8 cm, at apex acuminate with slender tips 1–1.5 cm long, at base cuneate to obtuse or somewhat rounded, papyraceous, adaxially glabrous, abaxially puberulous especially on costa and secondary veins; secondary veins 9–12 pairs, usually looping widely to interconnect near margins, with 1–3 intersecondary veins usually present between pairs of secondary veins, adaxially costa prominulous and remaining venation reticulated and raised, abaxially costa prominulous to prominent, secondary veins prominulous, and minor venation raised; margins thinly cartilaginous; *petioles* 1–2 cm long, glabrous; *stipules* glabrous, united around the stem in a continuous truncate sheath 1.5–3 mm long, lobes deltoid to ligulate, 1–1.5 mm long, acute to obtuse, entire. *Inflorescences* erect, often tripartite and apparently sessile; peduncles 4.5–10 cm long; panicles pyramidal, 10.5–15 × 10–16 cm excluding corollas, with secondary axes 5–8 pairs, with flowers pedicellate in cymules of 3–9; bracts triangular to narrowly so, acute, entire to ciliolate, those subtending secondary axes 3–5 mm long, those subtending or borne along pedicels 0.3–1 mm long; pedicels 2–4 mm long; peduncle, axes, bracts, and pedicels glabrous, yellow; *flowers* apparently distylous, with hypanthium turbinate to ellipsoid, somewhat flattened, glabrous, ca. 1 mm long; *calyx* limb glabrous, 0.5–1 mm long, divided for ¼–½ of its length, lobes deltoid, entire to ciliolate; *corolla* tubular, white, at base swollen and somewhat gibbous, somewhat bent there, generally straight in tube, externally glabrous, internally glabrous except for a pilose ring ca. 1.5 mm wide just above basal swelling, tube ca. 11 mm long, ca. 2.5 mm diam. near middle, lobes triangular, 2.5–3 mm long, acute, sometimes somewhat thickened at apex; *anthers* in long-styled form included, positioned at ca. ¾ of length of tube above base, ca. 2.5 mm long; *stigmas* in long-styled form exserted, ca. 0.8–1 mm long; *disk* ca. 1 mm high. *Infructescences* apparently similar to inflorescences; *fruit* ellipsoid to somewhat obovoid, laterally flattened, ca. 4 × 4.5 mm; *pyrenes* with low angled longitudinal ridges. Wet forest at 450–1440 m, southern Colombia to Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its stipules with continuous truncate sheaths and relatively short lobes, pyramidal yellow inflorescences, relatively short, shallowly lobed calyx limb, and white corollas. It is similar to *Palicourea thyrsiflora*, which has yellow to orange or red inflorescence branches and corollas. One fruiting specimen, *Jørgensen 56420*, is provisionally placed here; if this is correct, then *P. luteonivea* also differs from *P. thyrsiflora* in its ellipsoid to somewhat obovoid fruits with less marked ridges. *Palicourea luteonivea* may represent only a distinctive color form of *P. thyrsiflora*, but the consistent color differences support its recognition. The specific epithet refers to this distinctive combination of yellow inflorescence branches and white corollas. *Palicourea luteonivea* is also similar to *P. petiolaris* and *P. leuconeura*, with similarly colored flowers and inflorescences, but these latter species can be separated by their funnelform corollas that are bent strongly, to as much at 90°, in the lower part of the tube.

Paratypes. COLOMBIA. **Caquetá**: municipio de Florencia, carretera Florencia-Suaeza, Km 28, vereda "Las Brisas," 01°36′N, 75°37′W, *Ramírez et al. 4984* (JAUM, MO). ECUADOR. **Morona-Santiago**: eastern slopes of the Cordillera, valley of Ríos Negro and Chupianza (on trail from Sevilla de Oro to Méndez), *Camp 829* (S); Cordillera Cutucú, ridge just S and W of Río Itzintza, ca. 02°40′S, 78°W, *Camp 1292* (S); road Limón-La Unión, Km 10–12, *Harling 26048* (GB); Bomboiza, Misión Salesiana Shuar, 03°25′S, 78°35′W, *Neill et al. 7401* (MO). **Zamora-Chinchipe**: Valladolid, track NW of village, 04°34′S, 79°08′W, *Jørgensen 56420* (AAU); Nangaritza, Pachicutza, camino al Hito, Cordillera del Cóndor, 04°07′S, 78°37′W, *Palacios et al. 8348* (MO, QCNE).

Palicourea prodiga Standley ex C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: cantón de Quijos, margen derecha del Río Cosanga, 3 km arriba del puente de Cosanga, 00°36′S, 77°52′W, 18 Oct. 1990, *W. Palacios 6385* (holotype, MO-5006739; isotype, QCNE not seen). Figure 6F, G.

Haec species a *Palicourea* flavescente foliis stipulisque sat amplis, partibus omnibus pubescentia densa vestitis atque inflorescentia floribusque luteis distinguitur.

Flowering at 2 m tall, to 4 m tall; stems densely hirtellous to usually hirsute. *Leaves* paired; *blades* elliptic to somewhat broadly so, 13.5–28 × 6.5–18 cm, at apex acuminate with deltoid to slender tips 8–25 mm long, at base cuneate to obtuse or rounded, papyraceous, hirtellous throughout, usually more densely so on costa and secondary veins; secondary veins 19–27 pairs, spreading, broadly curved, generally extending to unite with margins, with 1–3 intersecondary veins usually present between pairs of secondary veins, adaxially venation generally plane, abaxially costa prominent, second-

ary veins prominulous, and reticulated minor venation plane to usually thickened; margins thinly cartilaginous, sparsely to moderately ciliate; *petioles* 1–3.8 cm long, hirtellous to hirsute; *stipules* moderately to densely hirtellous to usually hirsute, united around the stem in a continuous truncate sheath 8–22 mm long, this generally quadrate, costate on the angles, weaker in interpetiolar portions and frequently splitting there, the costate angles terminating in narrowly triangular to linear lobes 6–10 mm long, acute. *Inflorescences* erect; peduncles 3.5–7 cm long; panicles pyramidal, 10–19 × 7.5–19 cm excluding corollas, with secondary axes 8–10 pairs, with flowers pedicellate in cymules of 5–11; bracts triangular to narrowly so or lanceolate, obtuse to acute, entire to ciliolate, those subtending secondary axes 2–16 mm long, those subtending pedicels 1–2 mm long; pedicels 1–3 mm long; peduncle, axes, bracts, and pedicels densely pilosulous to hirtellous, pale green to yellow; *flowers* distylous, with hypanthium turbinate, sparsely hirtellous, ca. 1 mm long; *calyx* limb sparsely to moderately hirtellous, 0.8–1.2 mm long, divided for ½–⅔, lobes triangular to deltoid, acute, ciliolate; *corolla* funnelform, yellow, a little swollen at base, generally straight there, straight to slightly curved in tube, externally sparsely to moderately hirtellous, internally glabrous except for a pilose ring ca. 0.5 mm wide at ca. ⅓ of length of tube above base, tube 5–6 mm long, ca. 1.5 mm diam. near middle, lobes triangular to ligulate, 2.5–3 mm long, acute; *anthers* in long-styled form ca. 1.2 mm long, just included, in short-styled form ca. 1.5 mm long, exserted; *stigmas* in long-styled form ca. 1 mm long, exserted, in short-styled form ca. 2.5 mm long, positioned ca. ⅔ of length of tube above base; *disk* ca. 1 mm high. *Infructescences* similar to inflorescences except color unknown; young *fruit* ellipsoid, perhaps somewhat flattened laterally, ca. 4.5 × 4.5 mm; *pyrenes* with 3–5 low rounded longitudinal ridges. Wet forests at 2100–2900 m, central Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. d.]

This species is distinguished by its relatively large leaves, relatively large stipules with costate quadrate sheaths and narrow lobes, dense pubescence on all parts, yellow inflorescences, and yellow relatively short corollas. The corollas appear to be unusually short for *Palicourea*, but while those of one specimen (*Ownbey 2663*) are 5–6 mm long, the collection notes describe the tubes in the field as "12 mm long," indicating that the corollas of this species shrink significantly when dried. *Palicourea prodiga* is similar to *P. flavescens*, which has smaller leaves and stipules, pilosulous rather than hirtellous or hirsute pubescence, flowers white to yellow becoming blue when old, and a generally higher elevational range, 2785–3200 m. This specific epithet was proposed by Standley in sched. but never published; it apparently refers to the unusually large leaves and stipules. Standley also wrote this name on several specimens that are here excluded from *P. prodiga*, in particular specimens of a purple-flowered plant from Peru with somewhat spathaceous stipules.

Paratypes. ECUADOR. **Napo**: slopes of Guagra Urcu, on the loma above upper Río Borja, 00°28′S, 77°44′W, *Holm-Nielsen et al. 27026* (AAU); upper slopes of Guagra Urcu, 00°28′S, 77°44′W, *Holm-Nielsen et al. 27163* (AAU), *27250* (AAU); Guagra Urcu, the pass between Río Borja and Río Suno, 00°28′S, 77°43′W, *Holm-Nielsen et al. 27295* (AAU); upper Río Suno, near Guagra Urcu, 00°28′S, 77°42′W, *Holm-Nielsen et al. 27525* (AAU), *27550* (AAU); Quijos River region below Baeza, region of Río San Juan, 15 km NW of Chaco, *Ownbey 2663* (MO).

Palicourea subalatoides C. M. Taylor, sp. nov. TYPE: Ecuador. Pastaza: Misahuallí to Tena to Puyo to Mera, along road 65 km S of Tena, 01°05–29′S, 78°00′W, 19 Dec. 1986, *B. Hammel 16026* (holotype, MO-4990805). Figure 4A, B.

Haec species a congeneris stipularum vaginis truncatis ac lobulis bene evolutis lateraliter convexis, inflorescentia rotundato-corymbiformi ex rubra lutea, pedicello et limbo calycino bene evolutis atque corolla carnosa tubulari distinguitur.

Flowering at 1 m tall, to 8 m tall; stems with angles sharp to somewhat costate or shortly winged, glabrous to sparsely hirtellous. *Leaves* paired; *blades* elliptic, 5–22 × 2.5–8.2 cm, at apex acute to usually acuminate with slender tips 5–15 mm long, at base cuneate to acute and sometimes attenuate, papyraceous, adaxially glabrous, abaxially glabrous to sparsely hirtellous; secondary veins 7–21 pairs, usually extending at least weakly to margins, with 1(3) rather weak intersecondary veins usually present between pairs of secondary veins, adaxially costa thinly prominulous and remaining venation plane to a little thickened, abaxially costa prominent, secondary veins prominulous, and lesser venation plane to thickened; margins thinly cartilaginous; *petioles* glabrous to sparsely hirtellous, 4–10 mm long; *stipules* glabrous to sparsely hirtellous, united around the stem in a continuous truncate sheath 1.5–4 mm long, lobes triangular to slightly lanceolate, 4–16 mm long, acute, entire. *Inflorescences* erect, sometimes tripartite and apparently sessile; peduncles 1–8 cm long; panicles rounded-corymbiform, 1.5–6.5 × 2.5–9.5 cm excluding corollas, with secondary axes 2–4 pairs, as-

cending and usually equal to or exceeding the axis, with flowers pedicellate in cymules of 2–7; bracts entire, those subtending primary branches 5–10 mm long, triangular to lanceolate, acute, often with two short acute lobes at base, those subtending pedicels 1–3.5 mm long, narrowly triangular to lanceolate or oblanceolate, acute to obtuse; pedicels 3–10 mm long; peduncle, axes, bracts, and pedicels glabrous, red to orange or yellow; *flowers* distylous, with hypanthium cylindrical to cupuliform, glabrous, ca. 1.5 mm long; *calyx* limb glabrous, 2–3 mm long, divided for ca. ⅔–¾ its length, lobes ovate to elliptic or suborbicular, slightly imbricated, entire, obtuse to rounded; *corolla* tubular, yellow, slightly swollen and asymmetric at base, generally straight there and in tube, carnose, externally glabrous, internally glabrous except for a pilose ring ca. 2 mm wide at ca. ⅓ of length of tube above base, tube ca. 15 mm long, ca. 5 mm diam. near middle, lobes triangular to deltoid, ca. 1.5 mm long, acute, at apex a little thickened; *anthers* in long-styled form ca. 3.5 mm long, positioned ca. ⅔ of length of tube above base, in short-styled form ca. 3.5 mm long, partially exserted; *stigmas* not seen; *disk* ca. 1 mm high. Young *infructescences* similar to inflorescences; young *fruit* subglobose to obovoid, ca. 5 × 5 mm, glabrous; *pyrenes* with very low, perhaps rather sharp longitudinal ridges. Wet forest at 800–1160 m, eastern slopes of Andes in central to southern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its stipules with relatively well-developed, truncate sheaths and well-developed triangular to lanceolate lobes, rounded-corymbiform red to yellow inflorescences, well-developed pedicels and calyx limb, and carnose tubular corollas. It is similar to *Palicourea subalata*, which has narrowly triangular stipule lobes 2–6.5 mm long, calyx limb 0.5–1.5 mm long with narrowly triangular lobes that are unequal on an individual flower, and less carnose corollas with lobes that are thickened abaxially at apex. The specific epithet refers to this similarity. The corollas appear to elongate in the tube markedly shortly before anthesis.

Paratypes. ECUADOR. **Morona-Santiago**: 2–4 km N of Arapicos, *Lugo 5955* (GB, MO); 2–6 km S of Arapicos, *Lugo 5989* (GB, MO). **Napo**: cantón Gonzalo Pizarro, río Tigre, afluente del río Dashiño, de la carretera Lumbaqui-Reventador, Km 73, 10 km al S, 00°05′S, 77°24′W, *Neill & Palacios 7666* (MO). **Pastaza**: Mera, *Asplund 18928* (S); along road between Puyo and Diez de Agosto and Arajuno, 18 km NE of main Puyo-Macas road (beginning 3.7 km from center of Puyo at Hotel Europa), 8.2 km NE of Diez de Agosto, 01°27′S, 77°51′W, *Croat 59024* (MO); cantón Pastaza, between Shell and Mera, 5.3 km NW of center of Shell, along gravel road 1.1 km N of highway, 01°27′S, 78°04′W, *Croat 73527* (MO); Shell-Mera, *Fagerlind & Wibom s.n.* (S); 3.5 km N of Puyo, *Fagerlind & Wibom 1193* (S); 2 km from Puyo, road to Tena, *Harling 3235* (S); Mera, Allpayacu, *Harling 3342* (S); Mera, *Harling 3728* (S); Puyo-Puerto Napo road, San José ca. 17 km NE of Puyo, *Harling & Andersson 17107* (GB); ca. 18 km E of town of Río Negro towards Puyo, *Humbles 6103* (MO); Puyo-Macas road, 5 km after Veracruz, 01°33′S, 77°54′W, *Jørgensen & Lægaard 56476* (AAU); Canelos, *Lugo 4493* (GB, MO); 10–20 km N of Canelos, *Lugo 4579* (GB, MO); Puyopungo-Pomona, ca. 3 km E of Puyopungo, *Lugo 5124* (GB, MO); Hacienda San Antonio de Barón von Humboldt, 2 km al NE de Mera, 01°27′S, 78°06′W, *Neill et al. 6117* (MO); Madre Tierra, between Hacienda Zulay and Río Pastaza, 01°34′S, 78°02′W, *Øllgaard 99587* (AAU); 5 km al NE de Mera, carretera al río Anzu, 01°26′S, 78°06′W, *Palacios et al. 171* (MO); Km 10 on Puyo-Puerto Napo road, 01°25′S, 78°00′W, *Stein 2994* (MO).

Palicourea subtomentosa (Ruiz & Pav.) C. M. Taylor, comb. nov. Basionym: *Psychotria subtomentosa* Ruiz & Pav., Fl. peruv. 2: 61, t. 210, fig. a. 1799. *Cephaëlis subtomentosa* (Ruiz & Pav.) Spreng., Syst. veg. 1: 749. 1825. TYPE: Peru. Huánuco: "in Peruviae Andinae montibus nemorosis ad Chinchao, Mesapata et Maychainio runctationes, fl. Jun et Jul," *Ruiz & Pavón s.n.* [type, MA not seen photo (Rockefeller/F neg. # 29657) MO].

Palicourea subtomentosa is distinguished by its usually relatively small vegetative parts with pilosulous to hirtellous pubescence throughout, broadly pyramidal to rounded inflorescences, and pilosulous funnelform corollas with tubes 6–10 mm long. It is similar to *P. buchtienii*, and these two species were apparently confused by Standley in his original description of that species. *Palicourea buchtienii* is distinguished from *P. subtomentosa* by its glabrescent leaves, white to yellow corollas that are moderately pilosulous to glabrous externally with tubes 11–14 mm long and lobes with cylindrical abaxial appendages 0.3–0.8 mm long, and yellow inflorescence branches; in the areas where *P. buchtienii* and *P. subtomentosa* both grow, *P. subtomentosa* has blue flowers and inflorescences. Standley (1936) treated *Psychotria subtomentosa* as a poorly known species of *Psychotria* that was narrowly endemic in Peru, apparently overlooking the pilose ring inside the poorly preserved corollas on the specimens that he examined. Based on this feature and supported by the colored inflorescences and corollas, this species is here transferred to *Palicourea*. Two subspecies of *Palicourea tomentosa* are here distinguished:

1. Inflorescences blue to purple or lavender with the

internodes of the primary axis usually at least shortly developed; corollas blue to purple or lavender, or white with blue or purple trichomes; northern Peru to central Bolivia, in cloud forest at 1900–3400 m..... *Palicourea subtomentosa* subsp. *subtomentosa*

1. Inflorescences yellow, with the internodes of the primary axis usually hardly developed; corollas yellow to white with the trichomes not colored or perhaps yellow; southern Ecuador, in wet forest at 2210–2700 m..... *Palicourea subtomentosa* subsp. *lojana*

Palicourea subtomentosa subsp. **lojana** C. M. Taylor, subsp. nov. TYPE: Ecuador. Zamora-Chinchipe: above Valladolid on road to Yangana, 2300 m, 1 Feb. 1985, *G. Harling & L. Andersson 21367* (holotype, MO-4278926; isotype, GB). Figure 2B.

Haec subspecies a subspecie typica inflorescentiae ramis luteis atque corolla ex lutea alba differt; in Aequitoris australi tantum crescit.

Flowering at 0.5 m tall, to 5 m tall; stems sometimes weak to clambering, often suffrutescent, moderately to usually densely pilosulous to hirtellous. *Leaves* paired; *blades* elliptic, 4–15 × 1.2–6 cm, at apex acute to infrequently acuminate with tips ca. 5 mm long, at base acute to infrequently cuneate, papyraceous, moderately to densely pilosulous throughout, usually more densely so on costa and secondary veins; secondary veins 5–15 pairs, usually uniting with margins or infrequently looping to interconnect, without or sometimes with 1–2 weak intersecondary veins present between pairs of secondary veins, adaxially venation plane or costa slightly raised, abaxially costa and secondary veins prominulous and minor venation plane or thickened; margins thinly cartilaginous, entire; *petioles* moderately to densely hirtellous or pilosulous, 3–12 mm long; *stipules* moderately to densely hirtellous to pilosulous, united around the stem in a continuous sheath 1.5–3 mm long, lobes narrowly triangular, 1.5–3 mm long, acute, entire to slightly erose, with sinus concave to subtruncate. *Inflorescences* erect or perhaps somewhat deflexed; peduncles 2.5–4.5 cm long; panicles broadly pyramidal to usually broadly rounded, 1.5–3 × 3–5 cm, with secondary axes 1–3 pairs, with lower internodes of primary axis shortly or hardly expanded and secondary axes appearing subverticillate, with flowers sessile to shortly pedicellate together in cymules of 5–7; bracts narrowly triangular to linear, acute, those subtending secondary axes 3–6 mm long, those subtending flowers 0.8–2 mm long; pedicels 0–2.5 mm long; peduncle, axes, bracts, and pedicels moderately to densely pilosulous to hirtellous, yellow; *flowers* distylous, with hypanthium turbinate to cylindrical, moderately to usually densely pilosulous, 0.6–1 mm long; *calyx* limb moderately to densely pilosulous, 0.6–1.2 mm long, lobed for ca. ½–⅔, lobes deltoid to narrowly triangular or ovate, acute, sometimes unequal on an individual flower; *corollas* funnelform, white to yellow, slightly swollen at base, straight there and in tube, externally densely pilosulous with trichomes often blue or purple, internally glabrous except for a rather diffuse villous ring ca. 2 mm wide, tube 6–10 mm long, 1.1–1.2 mm diam. near middle, lobes triangular, 1.2–2 mm long, at apex smooth or sometimes with thickened projections to ca. 0.3 mm long abaxially; *anthers* in short-styled form ca. 3 mm long, partially exserted; *stigmas* in short-styled form ca. 1.5 mm long, positioned near middle of tube, in long-styled form ca. 0.3 mm long, exserted; *disk* 0.8–1 mm long. *Infructescences* similar to inflorescences or often with internodes of primary axis expanding; *fruit* ellipsoid, 5–6 × 4.5–5 mm, laterally flattened, pilosulous, blue; *pyrenes* with 3–5 distinct longitudinal angles. Wet forest at 2210–2700 m, southern Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

Plants from southern Ecuador differ from plants of Peru and Bolivia only in this separate geographic range and their inflorescence development and inflorescence and corolla colors, which are yellow rather than blue to purple. No other features separate these two populations, nor is any gradual variation evident between them. Therefore, the plants from Ecuador are here recognized as a separate subspecies. The subspecific epithet commemorates the city and province of Loja, in the region from which this subspecies is known.

Paratypes. ECUADOR. **Loja**: Nudo de Sabanilla, northern part, *Harling et al. 20570* (GB, MO); Nudo de Sabanilla, western slope on road Yangana-Valladolid, *Harling & Andersson 21789* (GB); Nudo de Sabanilla, western slope, ca. 10 km above Yangana on road to Valladolid, *Harling & Andersson 23620* (GB); Cerro Toledo, road to "La Torre" ca. 7 km SE of Yangana, *Harling & Andersson 23825* (GB, MO); Cerro Bangala, ca. 10 km E of Yangana, *Harling 25328* (GB). **Zamora-Chinchipe**: cantón Zamora, Podocarpus National Park near El Tambo, 40 km NW of Zamora on road to Loja, 03°58′S, 79°07′W, *Gentry 79947* (MO).

Palicourea ulloana C. M. Taylor, sp. nov. TYPE: Ecuador. Morona-Santiago: 17–18 km N of Gualaquiza on road to Indanza, 17 Apr. 1985, *G. Harling & L. Andersson 24226* (holotype, GB; isotype, MO-4278740). Figure 5A, B, C.

Haec species a congeneris stipularum vaginis membranaceis truncatis ac lobis cartilagineis coarctatis, inflorescentia ex anguste pyramidali cylindrica, limbo calycino

0.8–2.2 mm longo, corollae roseae rubraeve tubo 8–13 mm longo atque fructu pyrenas quattuor continente distinguitur.

Flowering at 0.5 m tall, to 2 m tall; stems often weak or clambering, moderately to densely hirsutulous sometimes becoming glabrescent with age. *Leaves* paired, *blades* elliptic, 4.5–14 × 1.4–5 cm, at apex acuminate with slender tips 0.8–1.8 cm long, at base acute to cuneate, papyraceous, adaxially glabrous or sparsely hirtellous along midrib, abaxially glabrous or moderately to densely hirtellous along midrib and sometimes on secondary veins; secondary veins 10–12 pairs, extending to unite with margins, with 1–2(3) intersecondary veins present between pairs of secondary veins, adaxially costa thinly prominulous, secondary veins thickened to prominulous, and reticulated minor venation plane to thickened, abaxially costa prominent, secondary veins prominulous, and minor venation plane to thickened; margins thinly to strongly cartilaginous; *petioles* glabrous to hirtellous, 3–10 mm long; *stipules* glabrous to hirtellous, united around the stem in a membranaceous, truncate sheath 1–2.5 mm long, sometimes splitting intrapetiolarly, interpetiolarly with a cartilaginous triangular portion 2–3 mm long, this costate on margins and terminating in 2 closely set lobes 2–3.5 mm long, narrowly triangular, acute, entire to usually ciliolate. *Inflorescences* deflexed to pendulous; peduncles 3–9 cm long; panicles narrowly pyramidal to cylindrical, 3.5–10.5 × 2–3 cm excluding corollas, with secondary axes 4–8 pairs, not much developed, usually terminating in 1 cymule or solitary flowers, with flowers pedicellate in lax cymules of 2–3; bracts triangular to narrowly so, entire to ciliolate, acute, those subtending secondary axes 2–5 mm long, those subtending pedicels 1–3 mm long; pedicels 3–7 mm long; peduncle, axes, bracts, and pedicels glabrous to densely hirtellous, purple to red; *flowers* distylous, with hypanthium glabrous, ca. 1 mm long, turbinate to cupuliform; *calyx* limb glabrous, 0.8–2.2 mm long, divided nearly to completely to base, lobes narrowly triangular to narrowly ligulate, subequal to usually strongly unequal on an individual flower, acute, entire or ciliolate; *corolla* tubular to somewhat funnelform, red to pink or purple, slightly swollen at base, somewhat to strongly bent there, straight in tube, externally glabrous, internally glabrous except for a pilose ring ca. 1 mm wide at ca. ¼ of length of tube above base, tube 8–13 mm long, 2.5–4 mm diam. near middle, lobes 2–3 mm long, acute, triangular, a little thickened at apex; *anthers* in long-styled form ca. 3 mm long, positioned ca. ⅔ of length of tube above base, in short-styled form ca. 3 mm long, partially exserted; *stigmas* 4, in long-styled form ca. 1 mm long and just exserted, in short-styled form not seen; *disk* ca. 0.8 mm high. *Infructescences* similar to inflorescences; *fruit* oblate, ca. 4 × 3 mm, glabrous, blue; *pyrenes* 4, triangular with outer surface rounded, smooth. Wet and cloud forest at 1900–2600 m, north-central Ecuador to northern Peru. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its leaves with the secondary veins usually extending to the margins, which are rather thickened, its unusual stipules with a triangular cartilaginous portion terminating in closely set narrow lobes, narrowly pyramidal to cylindrical inflorescences with the branches simple, calyx limb 0.8–2.2 mm long with the lobes often strongly unequal on an individual flower, pink to red tubular to somewhat funnelform corollas, and oblate fruit with four pyrenes that are smooth on the outer surface. The four pyrenes and stigma lobes are unique in subgenus *Montanae*; the unusual stipule morphology resembles that of *Palicourea vulcanalis*. *Palicourea ulloana* is similar in aspect to *P. myrtifolia*, which has laminar stipules with broader lobes and corollas with tubes that are 5–9 mm long and gibbous and strongly bent at the base; and to *P. calantha*, which has calyx limbs 0.8 mm long and corollas yellow. This distinctive, attractive species is named in honor of Ecuadorian botanist Carmen Ulloa Ulloa, whose work has contributed significantly to our knowledge of the montane regions where *P. ulloana* lives.

Paratypes. ECUADOR. **Morona-Santiago**: road from Limón (General Plaza) to Cuenca, ca. 4 km above Plan del Milagro, 03°00′S, 78°30–40′W, *Stein 2833* (MO). **Napo**: cantón Quijos, Sierra Azul (Agrícola Industrial Río Aragón), colinas de Tundal, 00°40′S, 77°54′W, *Alvarez et al. 309* (MO, QCNE), *339* (MO, QCNE); cantón Quijos, parroquía de Baeza, comunidad de Santa Lucía de Bermejo, 00°31′S, 77°55′W, *Alvarez et al. 968B* (MO, QCNE); slopes of Guagra Urcu, on loma above upper Río Borja, 00°28′S, 77°44′W, *Holm-Nielsen et al. 26995* (AAU); carretera Baeza-Tena, a 17 km de Baeza en la localidad de Logma Playa, *Jaramillo et al. 12216* (GB); Quijos river region below Baeza, region of Río San Juan 15 km NW of Chaco, *Ownbey 2662* (MO); Archidona-Tena region, S of Río Parro, Cordillera de Guacamayos, W of Tena, *Ownbey 2740* (MO); cantón Quijos, Cosanga, Hacienda Guacamayos, Río Cosanga, microcuenca del Río Vinillos, 00°36′S, 77°51′S, *Palacios & Freire 5034* (MO). **Tungurahua**: El Mirador, Sierra de León, valley of Río Pastaza below Baños, *Steere & Camp 8274* (F). **Zamora-Chinchipe**: Nudo de Sabanilla-Valladolid, horse-trail to Caserío Quebrada Honda, *Harling 27144* (GB), *27177* (S); new road Loja-Zamora, trail to Podocarpus patch at Quebrada del Diablo, *van der Werff & Palacios 9241* (MO), *9240* (MO). PERU. **Amazonas**: Bagua province, ca. 20 km (by trail) E of La Peca, *Barbour 2818* (MO); Bagua

province, Cordillera Colán SE of La Peca, *Barbour 4161* (MO).

Palicourea vulcanalis Standl. ex C. M. Taylor, sp. nov. TYPE: Ecuador. Napo: Cordillera de Guacamayos above Urcusiqui on trail between Baeza and Tena, 6000 ft., 11 Mar. 1944, *M. Ownbey 2699* (holotype, F-1150284; isotype, MO-1600100). Figure 6B, C.

Haec species a congeneris stipularum vaginis bene evolutis ac lobulis coarctatis anguste lanceolatis 12–15 mm longis unoquoque glandulam ad basim gerente distinguitur.

Shrubs, height not recorded; stems glabrous or puberulous becoming glabrescent with age. *Leaves* paired; *blades* elliptic, 11.5–20 × 3–7.8 cm, at apex acuminate with slender tips 1.5–2 cm long, at base cuneate to acute, papyraceous, adaxially glabrous, abaxially puberulous throughout but more densely so on costa and secondary veins; secondary veins 10–14 pairs, generally looping to interconnect, with 1–2 weak intersecondary veins usually present between pairs of secondary veins, adaxially costa thickened to prominulous and lesser reticulated venation thickened, abaxially costa prominent, secondary veins prominulous, and minor venation thickened; margins thinly cartilaginous, entire; *petioles* glabrous to puberulous, 7–15 mm long; *stipules* glabrous to puberulous, united around the stem in a truncate continuous sheath 7–9 mm long, lobes narrowly to very narrowly lanceolate, 12–15 mm long, 1–2 mm wide near base, finely nerved, acute to acuminate, entire, closely set, each subtended at the leaf-side base by a gland 0.5–1.5 mm long, with sinus acute. *Inflorescences* apparently ascending or perhaps deflexed or with peduncle bent at base; peduncles 2–8 cm long; panicles pyramidal, 5–10.5 × 14–18 cm excluding corollas, with primary axis apparently sometimes flexuous, secondary axes 10–15 pairs, the basalmost frequently reflexed and ca. twice as long as next pair, with flowers pedicellate in cymules of 5–9; bracts narrowly triangular to linear, acute, those subtending secondary axes 6–18 mm long, those subtending flowers 3–6 mm long; pedicels 3–6 mm long; peduncle, axes, bracts, and pedicels puberulous, red; *flowers* with hypanthium glabrous, cylindrical, 1.2–1.5 mm long; *calyx* limb glabrous, 0.8–1.2 mm long, divided for ⅔ to most of its length, lobes lanceolate to ovate, obtuse to acute, often somewhat unequal on an individual flower; *corolla* funnelform, white, a little swollen at base, generally straight there and in tube, externally glabrous, internally glabrous except for a villous ring ca. 1 mm wide at ca. ⅓ of length of tube above base, tube ca. 8 mm long, ca. 1.2 mm diam. near middle, lobes triangular to deltoid, 1–1.2 mm long, acute; *anthers* in short-styled form ca. 1.2 mm long, positioned in throat, included or partially exserted; *stigmas* in short-styled form ca. 1.5 mm long, positioned ca. ⅔ of length of tube above base; *disk* ca. 0.5 mm high. *Infructescences* similar to inflorescences except violet; *fruit* ovoid, laterally flattened, ca. 5 × 4.5 mm, glabrous; *pyrenes* with 3–5 smooth angles. Wet forest at 1800–2000 m, east-central Ecuador. [Subg. *Montanae*, Sect. *Montanae*, Ser. 3, Subser. c.]

This species is distinguished by its unusual stipule morphology, with the truncate sheath well developed and the lobes closely set, relatively long and narrow, finely nerved, and each subtended on the leaf side by a gland to as much as 1.5 mm long. This stipule morphology is similar in general aspect to that of *Palicourea toroi* and *P. deviae*, but in both of these latter species the stipules are laminar and the lobes lack well-developed glands at the base. *Palicourea vulcanalis* is also distinguished by its relatively long inflorescences with the lowermost branches usually reflexed and about twice as long as the next pair, relatively long narrow bracts, white corollas with tubes ca. 8 mm long, ovoid laterally flattened fruits, and pyrenes with smooth angles rather than longitudinal ridges. This epithet was applied by Standley to the specimen designated here as the type, but never published; it apparently refers to the habitat of this species, in highlands of volcanic origin.

Paratype. ECUADOR. **Napo**: cantón El Chaco, margen derecha del río Quijos, Finca "La Ave Brava" de Segundo Pacheco, 00°12′S, 77°39′W, *Palacios 5395* (MO).

INDEX TO SPECIES CLASSIFIED

The position of each species in the classification is indicated by the numbers and letters following each name, which correspond to the numbers and letters designating the infraspecific taxa in the classification presented above. Asterisks (*) indicate names published in this work, above.

Palicourea abbreviata Rusby II, H, 8
Palicourea acanthacea C. M. Taylor II, I, 11
Palicourea acetosoides Wernham II, E, 3, c
Palicourea adusta Standl. II, F, 5
Palicourea affinis Standl. I, C, 2
Palicourea albert-smithii Standl. II, E, 4, e
Palicourea albocaerulea C. M. Taylor II, E, 4, f
Palicourea alpina (Sw.) DC. II, E, 3, c
Palicourea amapaensis Steyerm. I, B
Palicourea amethystina (Ruiz & Pav.) DC. II, E, 4, e
Palicourea amplissima (Standl. ex Steyerm.) C. M. Taylor II, F, 7
Palicourea andaluciana Standl. II, F, 7
Palicourea anderssoniana C. M. Taylor* II, E, 3, c
Palicourea andrei Standl. II, H, 9

Palicourea angustifolia Kunth II, E, 3, c
Palicourea anianguana C. M. Taylor* I, A
Palicourea anisoloba (Müll. Arg.) Boom & M. T. Campos I, c, 2
Palicourea antioquiana Standl. II, E. 4, f
Palicourea apicata Kunth II, F, 7
Palicourea aschersonianoides (Wernham) Steyerm. II, H, 8
Palicourea asplundii C. M. Taylor* II, F, 6
Palicourea attenuata Rusby I, A
Palicourea azurea C. M. Taylor* II, E, 4, f
Palicourea bella (Standl.) Dwyer II, I, 10
Palicourea bellula C. M. Taylor II, I, 10
Palicourea boyacana Standl. II, H, 9
Palicourea bracteosa Standl. I, C, 1, a
Palicourea brenesii Standl. II, E, 4, e
Palicourea buchtienii Standl. II, E, 3, c
Palicourea buntingii Steyerm. I, A
Palicourea calantha Standl. II, E, 3, c
Palicourea caloneura Rusby II, H, 8
Palicourea calophlebia Standl. II, E, 4, f
Palicourea calophylla DC. I, C, 2
Palicourea calothyrsus K. Schum. II, E, 3, c
Palicourea calycina Benth. II, E, 4, f
Palicourea canarina C. M. Taylor* II, E, 3, c
Palicourea candida C. M. Taylor* II, H, 9
Palicourea charianthema Standl. I, C, 1, a
Palicourea chignul C. M. Taylor* II, F, 6
Palicourea chimboracensis Standl. II, E, 4, e
Palicourea chiriquina Standl. II, F, 5
Palicourea condorica C. M. Taylor* II, I, 11
Palicourea conferta (Benth.) Sandw. I, C, 1, b
Palicourea coriacea Mart. I, C, 1, a
Palicourea corniculata C. M. Taylor* II, E, 3, c
Palicourea cornigera C. M. Taylor* II, E, 4, f
Palicourea corymbifera (Müll. Arg.) Standl. I, D
Palicourea crocea (Sw.) Roem. & Schult. I, C, 1, a
Palicourea croceoides Ham. I, C, 1, a
Palicourea cymosa (Ruiz & Pav.) DC. I, C, 1, b
Palicourea danielis Standl. II, E, 3, c
Palicourea demissa Standl. II, E, 4, e
Palicourea densa Standl. II, E, 4, f
Palicourea denslowiae J. H. Kirkbr. II, E, 4, g
Palicourea deviae C. M. Taylor II, E, 4, e
Palicourea dimorphandrioides C. M. Taylor II, I, 11
Palicourea discolor K. Krause II, E, 4, e
Palicourea dorantha Wernham II, E, 4, f
Palicourea eriantha DC. II, E, 3, c
Palicourea fastigiata Kunth I, C, 1, a
Palicourea flavescens Kunth II, E, 3, d
Palicourea flavifolia (Rusby) Standl. I, A
Palicourea frontinensis Cogollo & C. M. Taylor II, I, 11
Palicourea garciae Standl. II, H, 8
Palicourea gentryi C. M. Taylor* II, E, 3, c
Palicourea gibbosa Dwyer II, F, 6
Palicourea gomezii C. M. Taylor II, F, 7
Palicourea grandiflora Kunth I, B
Palicourea grandifolia Kunth I, A
Palicourea grandistipula (Standl. ex Steyerm.) C. M. Taylor II, I, 11
Palicourea guianensis Aubl. I, A
Palicourea hammelii C. M. Taylor II, I, 10
Palicourea harlingii C. M. Taylor* II, I, 11
Palicourea heilbornii Standl. II, E, 4, e
Palicourea herrerae Standl. II, E, 3, c
Palicourea herzogii Standl. I, C, 1, a
Palicourea heterantha Standl. II, E, 3, c
Palicourea heterochroma K. Schum. & K. Krause II, E, 4, f
Palicourea holmgrenii Standl. II, E, 3, c
Palicourea hospitalis Standl. II, F, 6
Palicourea huberi Steyerm. I, C, 1, a
Palicourea ionantha Standl. II, E, 3, c
Palicourea iquitoensis K. Krause I, C, 1, b
Palicourea irwinii Steyerm. I, D
Palicourea jahnii Standl. II, H, 8
Palicourea jaramilloi C. M. Taylor* II, E, 4, f
Palicourea justicioides Standley II, E, 4, f
Palicourea jatun-sachensis C. M. Taylor I, C, 1, b
Palicourea kalbreyeri Standl. II, F, 6
Palicourea killipii Standl. II, I, 10
Palicourea lachnantha Standl. I, A
Palicourea lancifera Standl. & L. O. Williams II, E, 4, f
Palicourea lancigera Steyerm. I, C, 1, a
Palicourea lasiantha K. Krause I, A
Palicourea lasiophylla Standl. I, C, 1, a
Palicourea lasiorrhachis Oerst. II, F, 5
Palicourea latifolia K. Krause II, E, 4, e
Palicourea lehmannii (Rusby) Standl. II, E, 4, e
Palicourea leucantha Donn. Sm. II, E, 3, c
Palicourea leuconeura Standl. II, H, 8
Palicourea linearifloria Wernham II, H, 9
Palicourea lineata Benth. II, G
Palicourea lobbii Standl. II, E, 3, c
Palicourea longepedunculata Gardner I, C, 2
Palicourea longiflora (Aubl.) A. Rich. I, C, 1, a
Palicourea longistipulata (Müll. Arg.) Standl. I, C, 1, a
Palicourea lugoana C. M. Taylor* II, F, 6
Palicourea luteonivea C. M. Taylor* II, E, 3, c
Palicourea lutulenta Standl. II, E, 3, c
Palicourea lyristipula Wernham II, F, 6
Palicourea macarthurorum C. M. Taylor* I, B
Palicourea macbridei Standl. II, I, 11
Palicourea macrantha Loes. II, H, 9
Palicourea macrobotrys (Ruiz & Pav.) DC. I, C, 2
Palicourea macrocalyx Standl. II, E, 4, f
Palicourea mansoana (Müll. Arg.) Standl. I, A
Palicourea marcgravii A. St.-Hil. I, C, 1, a
Palicourea melheana Jung-Mend. I, C, 2
Palicourea mello-barretoi Standl. I, C, 1, a
Palicourea mexiae Standl. II, F, 7
Palicourea montivaga Standl. II, F, 5
Palicourea myrtifolia K. Schum. & K. Krause II, F, 6
Palicourea nigricans K. Krause I, B
Palicourea nitidella (Müll. Arg.) Standl. I, C, 1, a
Palicourea nubigena Standl. II, F, 7
Palicourea obovata (Ruiz & Pav.) DC. II, G
Palicourea obtusata K. Krause II, F, 5
Palicourea ochnoides Dwyer II, I, 10
Palicourea officinalis Mart. I, C, 1, a
Palicourea orosiana C. M. Taylor II, F, 5
Palicourea orquidea C. M. Taylor II, I, 11
Palicourea ovalis Standl. II, E, 4, e
Palicourea pachycalyx Standl. I, A
Palicourea padifolia (Willd. ex Roem. & Schult.) C. M. Taylor & Lorence II, E, 3, c
Palicourea pauciflora Standl. II, F, 7
Palicourea pendula C. M. Taylor II, F, 5
Palicourea pennellii Standl. II, E, 3, c
Palicourea perquadrangularis Wernham II, E, 4, e
Palicourea petiolaris Kunth II, H, 8
Palicourea pittieri Standl. II, H, 8
Palicourea plowmanii C. M. Taylor I, C, 1, b
Palicourea ponasae K. Krause II, E, 3, c
Palicourea prodiga Standl. ex C. M. Taylor* II, E, 3, d
Palicourea psittacorum Standl. II, E, 3, c

Palicourea pulchra Griseb. II, H, 8
Palicourea punicea (Ruiz & Pav.) DC. I, C, 1, b
Palicourea purpurea C. M. Taylor II, E, 4, e
Palicourea quadrifolia (Rudge) DC. I, D
Palicourea quadrilateralis C. M. Taylor II, E, 4, g
Palicourea rigida Kunth I, A
Palicourea rigidifolia (Dwyer & M. V. Hayden) Dwyer II, E, 3, c
Palicourea salicifolia Standl. II, F, 7
Palicourea semirasa Standl. I, A
Palicourea skotakii C. M. Taylor II, I, 11
Palicourea sodiroi Standl. II, F, 6
Palicourea sopkinii C. M. Taylor II, I, 11
Palicourea spathacea C. M. Taylor II, I, 10
Palicourea standleyana C. M. Taylor II, E, 4, f
Palicourea stenosepala Standl. II, I, 10
Palicourea steyermarkii C. M. Taylor II, H, 8
Palicourea stipularis Benth. II, E, 4, e
Palicourea subalata Standl. ex Steyerm. II, E, 3, c
Palicourea subalatoides C. M. Taylor* II, E, 3, c
Palicourea subscandens Standl. ex Steyerm. II, G
Palicourea subspicata Huber I, C, 1 a
Palicourea subtomentosa (Ruiz & Pav.) C. M. Taylor* II, E, 3, c
Palicourea sulphurea (Ruiz & Pav.) DC. II, F, 7
Palicourea tamaensis (Standl. & Steyerm.) Steyerm. II, I, 11
Palicourea tectoneura K. Schum. & K. Krause II, E, 3, d
Palicourea tepuicola Steyerm. I, A
Palicourea tetraphylla Cham. & Schltdl. I, C, 2
Palicourea thermydri J. H. Kirkbr. II, E, 4, g
Palicourea thyrsiflora (Ruiz & Pav.) DC. II, E, 3, c
Palicourea tilaranensis C. M. Taylor II, H, 8
Palicourea toroi Standl. II, E, 4, f
Palicourea triphylla DC. I, C, 2
Palicourea tubuliflora Dwyer II, F, 7
Palicourea tumidonodosa Dwyer II, F, 7
Palicourea tunjaensis C. M. Taylor II, E, 4, f
Palicourea ulloana C. M. Taylor* II, E, 3, c
Palicourea vaginata Benth. II, F, 7
Palicourea vestita C. M. Taylor II, F, 5
Palicourea virens (Müll. Arg.) Standl. I, D
Palicourea vulcanalis Standl. ex C. M. Taylor* II, E, 3, c
Palicourea weberbaueri K. Krause II, E, 3, c
Palicourea wilesii C. D. Adams II, H, 8
Palicourea zarucchii C. M. Taylor II, H, 8

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PALYNOLOGY, PHYLOGENETIC RECONSTRUCTION, AND CLASSIFICATION OF THE AFRO-MADAGASCAN GENUS *ARISTEA* (IRIDACEAE)[1]

Peter Goldblatt[2] *and Annick Le Thomas*[3]

Abstract

Examination of the pollen grains of *Aristea* using light and scanning electron microscopy shows that this Afro-Madagascan genus of ca. 50 species is one of the palynologically most diverse genera of the family Iridaceae. Exine sculpturing ranges from reticulate to rugulate to areolate with lumina ranging from large to small. Overall size is also variable, with grains ranging from medium-sized (45–60 μm equatorial diameter) to large (70–97.5 μm equatorial diameter). Monosulcate apertures are plesiomorphic, and derived sulculate (apertural membranes obscured by masses of exine), zonasulculate, 2-zonasulculate, 3-sulcate, and spiral apertures are present in various species. Pollen characters were combined with morphological and anatomical features in a matrix and subjected to cladistic analysis. Trees obtained using successive weighting procedures were used as the basis for a revised infrageneric classification of *Aristea* in which three subgenera are recognized. Two subgenera are restricted to the winter-rainfall zone (the Cape Floristic Region) of southern Africa, and the third is dispersed widely across sub-Saharan Africa and Madagascar but is barely represented in the Cape Region. Apomorphic character states are discussed in relation to the biology of the genus, and we suggest that some derived aperture types may be adapted to the desiccating climate of the Cape Region.

Information now available on various aspects of the pollen morphology of the Afro-Madagascan genus *Aristea* indicates that it is among the most variable genera of Iridaceae (if not the most variable) as regards pollen-grain apertures and exine sculpturing. The first reports of pollen morphology in *Aristea* (Radelescu, 1970; Schulze, 1971a), using light microscopy, made it clear that the genus was unusual palynologically. More detailed study using scanning electron microscopy (SEM) of six species occurring on Madagascar (Straka & Friedrich, 1984; Goldblatt & Le Thomas, 1992a) confirmed the apertural diversity, even in this limited geographical area and with the low species diversity for the genus. With some 50 species (Weimarck, 1940; Vincent, 1985; Goldblatt, 1995a, 1995b; Goldblatt & Manning, 1997), *Aristea* is the largest of the six genera of Nivenioideae, one of four subfamilies currently recognized in Iridaceae (Goldblatt, 1990, 1993). *Aristea* is unusual in Iridaceae in having a particularly wide geographic range. It is one of only a handful of the 35 African genera of the family that extend across all of sub-Saharan Africa, and one of only three that are shared with Madagascar, the others being *Crocosmia* (9 spp: 1 in Madagascar) and *Gladiolus* (ca. 255 spp: 8 in Madagascar), both members of subfamily Ixioideae. *Aristea* is also among the most variable genera of Iridaceae as regards fruit and seed morphology. In this paper we extend our earlier palynological survey of *Aristea* to the African species and combine the variation in pollen-grain characters with features of fruit, seeds, and other morphological structures in a cladistic analysis in order to increase our understanding of the phylogeny of the genus. The results provide valuable insights into the evolution and geographic radiation of the genus and are used to refine the infrageneric classification.

Materials and Methods

Palynology

Pollen samples (Table 1) of 32 of the estimated 50 species of *Aristea* were collected in the wild,

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[2] B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

[3] E.P.H.E., Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, 16 rue Buffon, Paris 75005, France.

Table 1. Species of *Aristea* examined, with voucher data and pollen grain dimensions. Voucher specimens are located at MO, with additional duplicates often at NBG, P, and PRE (herbarium acronyms after Holmgren et al. (1990)); collectors are abbreviated as follows G = Goldblatt, M = Manning. Species are arranged alphabetically within the sections recognized by Weimarck (1940). *Aristea fimbriata*, unknown to Weimarck, is assigned to section *Racemosae*, where he would presumably have placed it.

Taxon	Grain size, μm	Voucher information
Section *Singulares* Weim.		
A. singularis Weim.	59.1 × 51.0	S. Africa, W. Cape, *Taylor 11009* (MO)
Section *Eucapsulares* Goldblatt (= sect. *Euaristea* Weim.)		
A. angolensis Baker	60.0 × 58.5	S. Africa, Natal, *G & M 8360; 9818; 9870*
A. grandis Weim.	54.3 × 51.6	S. Africa, Natal, *G & M 9857*
A. montana Baker	60.0 × 57.0	S. Africa, Natal, *G & M 9858*
A. nyikensis Baker	61.0 × 51.0	Malawi, *Bidgood et al. 1310*
A. polycephala Harms	51.0 × 45.0	Tanzania, *la Croix 4267*
A. ranomafana Goldblatt	57.7 × 40.0	Madagascar, *Malcomber 1336*
A. schizolaena Harv.	66.7 × 60.0	S. Africa, E. Cape, *G & M 9588*
A. woodii N. E. Br.	59.5 × 56.5	S. Africa, E. Transvaal, *G & M 9815; 9831*
(*A. angustifolia* Baker, *A. humbertii* H. Perr., *A. kitchingii* Baker, and *A. madagascariensis* Baker (Goldblatt & Le Thomas, 1992a) all have grains smaller than 60 μm equatorial diameter.)		
Section *Trilobatae* Weim.		
A. platycephala Baker	60.6 × 59.6	S. Africa, E. Cape, *van Wyk & Mathews 7727*
Section *Ancipites* Weim.		
A. abyssinca Pax	63.3 × 55.5	S. Africa, Natal, *G & M 9855*
A. anceps Ecklon	54.0 × 46.9	S. Africa, E. Cape, *G & M 9530*
Section *Cladocarpae* Weim.		
A. cladocarpa Baker	48.5 × 45.0	Madagascar, *Bosser 16695* (see also Goldblatt & Le Thomas, 1992a)
Section *Pseudaristea* Pax		
A. biflora Weim.	71.2 × 70.5	S. Africa, W. Cape, *Goldblatt 8898*
A. cantharophila Goldblatt & J. Manning	69.2 × 66.4	S. Africa, W. Cape, *G & M 10284*
A. ecklonii Baker	63.0 × 59.0	S. Africa, E. Cape, ex hort
A. lugens (L.f.) Weim.	92.2 × 81.0	S. Africa, W. Cape, *Oliver 4739*
A. pauciflora W. Dod.	73.5 × 63.5	S. Africa, W. Cape, *G & M 10102*
A. pusilla (Thunb.) Ker	59.6 × 58.5	S. Africa, W. Cape, *Bayliss 7635*
A. simplex Weim.	71.1 × 67.5	S. Africa, W. Cape, *G & M 9754*
A. spiralis (L.f.) Ker Gawl.	73.5 × 63.5	S. Africa, W. Cape, *G s.n.* (Cape Point)
A. teretifolia Goldblatt & J. Manning	79.3 × 77.1	S. Africa, W. Cape, *Bean 2785; Nanni s.n.*
A. sp. *? aff. pauciflora*	81.2 × 76.2	S. Africa, Cape, *Drewe 466*
Section *Racemosae* Weim.		
A. confusa Goldblatt	54.0 × 51.1	S. Africa, W. Cape, *G s.n.* (Hout Bay)
A. fimbriata Goldblatt ined.	73.5 × 70.5	S. Africa, W. Cape, *G & M 10167*
A. juncifolia Baker	52.7 × 45.0	S. Africa, W. Cape, *Williams 891; Orchard 354*
A. major Andrews	45.0 × 42.0	S. Africa, Cape, *G s.n.* (Hout Bay)
A. monticola Goldblatt	54.0 × 49.5	S. Africa, W. Cape, *G & M 9476A*
A. racemosa Baker	52.5 × 48.0	S. Africa, Cape, *Oakes s.n.*
Section *Aristea*		
A. africana (L.) Hoffmsg.	95.2 × 92.2	S. Africa, W. Cape, *G & M 9352*;
	82.5 × 81.0	*G & M 9505*;
	87.0 × 83.2	*Bean 2789*;
	88.5 × 77.2	*G & M 9750*
A. dichotoma (Thunb.) Ker Gawl.	97.5 × 93.0	S. Africa, W. Cape, *G & M 9503; G & M 10154*
A. glauca Klatt	82.5 × 75.0	S. Africa, W. Cape, *G & M 9595A*
A. oligocephala Baker	97.5 × 85.5	S. Africa, W. Cape, *Barker 412*

fixed in FAA, and subsequently stored in 70% ethanol, or were taken from herbarium specimens in the collections at the Laboratoire de Phanérogamie, Paris (P), or the Missouri Botanical Garden, St. Louis (MO). All samples were examined under the light microscope (LM), without acetolysis, and mounted in glycerine jelly, but after rehydration of anthers in a wetting agent and subsequent washing for herbarium samples. For SEM study, non-acetolyzed rehydrated herbarium samples and spirit material were fixed in 2.5% glutaraldehyde solution, washed in a 0.1 M cacodylate buffer, then dehydrated and critical-point dried. Pollen of *Aristea* is difficult to study owing to the fragility of the exine, of which the foot layer is extremely thin. It is important to examine non-acetolyzed grains under the light microscope in the hydrated, or rehydrated, state so that the apertures can be more clearly interpreted by the presence of thickened intine. In some cases, acetolyzed grains were examined in LM to amplify our observations. Grain size (Table 1) is the average of measurements of 10 grains mounted in glycerin jelly. The terminology used is, as far as possible, in accordance with the *Glossary of Pollen and Spore Terminology* (Punt et al., 1994) and the special sulcus types described for monocots by Halbritter and Hesse (1993).

PHYLOGENETIC ANALYSIS

Aristea is relatively uniform in floral morphology, fairly diverse in the arrangement of the inflorescence units (binate rhipidia) on the flowering stem, and remarkably variable in capsule and seed morphology. The current classification of the genus into eight sections is based largely on fruit and seed characters (Weimarck, 1940). Species are, however, recognized in many instances on inflorescence characters and sometimes on the basis of vegetative features including overall size and stem compression. Using Weimarck's monograph of the genus as the primary source of morphological data, supplemented where necessary from herbarium material and new observations (Goldblatt, 1995a; Goldblatt & Manning, 1997), we have identified 24 phylogenetically informative morphological features (Appendix 1). These have been polarized exclusively using outgroup comparison. Some of the features are quantitative multistate characters that arguably should not be included in a phylogenetic analysis. We believe they do have some phylogenetic information and are readily polarized; hence we have included them. Our outgroup is a combined one, four of the remaining five genera of subfamily Nivenioideae (Goldblatt, 1990, 1993). These are the Australasian *Patersonia* and three shrubby southern African genera, *Klattia*, *Nivenia*, and *Witsenia*. Where characters in the outgroup genera are not congruent, we determined the ancestral state by comparing the character to genera of Iridaceae outside the subfamily. A sixth genus of Nivenioideae, *Geosiris*, was not taken into consideration for character polarization because it is a highly specialized, leafless and achlorophyllous plant, most features of which have no homologue in *Aristea*.

We also included two nontraditional characters in the analysis, one from leaf anatomy and one relating to floral nectaries. The outgroup genera have leaves with strands of subepidermal sclerenchyma in the leaf margins (Rudall & Burns, 1989), but the seven species of *Aristea* known anatomically lack this tissue (Rudall, 1995; J. Manning, pers. comm.), instead having columnar epidermal cells with thickened anticlinal walls. Both anatomical conditions are probably universal for the genus but are scored only for the species in which they are known. Septal nectaries are considered to be the plesiomorphic condition in Nivenioideae (Goldblatt, 1993). They occur in *Patersonia* (P. Rudall, pers. comm.) and in *Nivenia*, *Klattia*, and *Witsenia* (Goldblatt, 1993). Flowers of nearly all species of *Aristea* lack nectar (unpublished observations), but *A. spiralis* does secrete nectar, which has been found to be produced from perigonal nectaries located near the tepal bases (J. Manning, pers. comm.), an autapomorphy for that species. The above three characters contain no information relevant to the relationships of members of the ingroup but seem unambiguously to establish the monophyly of *Aristea*, which has few apomorphic morphological features. The only apparent specialized feature in *Aristea* is the vestigial perianth tube. Papillate outer epidermal cells of the seed coat, present in the few species examined for the character, may be another. No other genus of Iridaceae is known to have such epidermal cells in the seed coat (unpublished data).

Characters of the species of *Aristea* examined here were combined with data for several more for which there is palynological information (Goldblatt & Le Thomas, 1992a), assembled in a matrix (Table 2), and analyzed using the Hennig86 package of programs for phylogenetic analysis (Farris, 1988). The data set, including 33 characters and up to 36 taxa, took considerable time to run using the ie option (generating trees by implicit enumeration). We thus decided to use the mh* bb* options for the analysis, which applies branch swapping to each of the initial trees and saves all the shortest trees generated. Tree lengths, and consistency and

Table 2. Data matrix and character list for *Aristea*. Multistate characters are 1, 4, 9, 11, 12, 13, 14, 15, 18, 19, 20, 24, and 33; of these 4, 9, 12, 14, and 18 are additive or arbitrarily divided grades in a more or less continuous range of variation and are treated as ordered states. Characters are scored ? if unknown or intermediate between two states [Note: some scorings change for the matrix that includes Ixioideae, and an additional character, 34, is added for this analysis.]

1. Pollen grain apertures restricted to one surface, usually monosulcate, rarely trichotomosulcate (0)—grains sulculate (1); 2-zonasulculate (2); grains 3-sulcate or spiraperturate (3)
2. Aperture membrane smooth to granular, without exine fragments (0)—aperture membrane with exine fragments, sometimes forming an operculum-like median band (1)
3. Aperture border not diffuse (0)—aperture border diffuse (1)
4. Exine lumina large (0)—medium-sized (1); small (2)
5. Exine surface (muri or areolae) smooth (0)—exine surface sculpted (1)
6. Exine surface without perforations (0)—surface with perforations (1)
7. Pollen grains smaller (diameter less than 65 μm) (0)—larger (diameter more than 70 μm) (1)
8. Pollen always shed in monads (0)—pollen often shed in tetrads (1)
9. Exine reticulate (0)—rugulate (1); rugulo-areolate (2)
10. Rhipidial spathes prominent, enclosing the entire inflorescence (0)—spathes not prominent and buds and floral bracts evident (1)
11. Capsules round to lightly 3-lobed in section (0)—capsules 3-winged (1); capsules 3-lobed (2); deeply divided into 3 lobes, each widest in the middle (3)
12. Capsules in profile more or less ovoid (0)—capsules oblong (1); capsules elongate (2)
13. Capsule walls brittle and dehiscing normally (0)—walls thin, dehiscing on the septa (1); walls thick and woody, tardily dehiscent (2)
14. Seeds numerous to several per locule (0)—seeds usually 4 per locule (1); seeds 2 per locule (2)
15. Seeds rounded to prismatic (0)—seeds radially compressed (1); seeds nearly cylindric and obliquely truncate at both ends (2); seeds globose with an aril (3)
16. Anthers ovoid-oblong (0)—anthers narrrow and linear (1)
17. Anthers longitudinally dehiscent (0)—anthers apically dehiscent (porose) (1)
18. Lateral rhipidia all terminal on branches, thus stalked (0)—some lateral rhipidia sessile (1); all lateral rhipidia normally sessile (2)
19. Compound inflorescence racemose, spicate, or subpaniculate (0)—subdichotomously branched (1); 1–2 subterminal flower clusters (2)
20. Stem lightly compressed to terete in upper half (0)—stem strongly compressed and broadly winged throughout (1); narrow and ancipitous (2)
21. Outer tepal whorl similar to inner (0)—outer and inner whorls differentiated in size and color (1)
22. Flowers more or less upright (0)—flowers secund (1)
23. Style lobed apically and the lobes fringed (0)—style minutely notched apically (1)
24. Rhipidial spathes and floral bracts green to brownish and chartaceous (0)—spathes and bracts silvery and scarious with entire margins (1); with regularly fringed, rust-colored margins (2)
25. Septal nectaries present (0)—septal nectaries absent (1)
26. Flowering stem bearing a few leaves decreasing in size above (0)—basal internode very long, leafless except for a subterminal bract-like leaf (1)
27. Flowering stems exceeding the leaves and plants not cushion-like tufts (0)—flowering stems short and plants low cushion-like tufts (1)
28. Inflorescences with several to few flower clusters (0)—compound inflorescence massively enriched (1)
29. Seed surface with primary sculpturing, usually rugose (0)—surface without primary sculpturing (1)
30. Leaf margins with subepidermal sclerenchyma (0)—without subepidermal sclerenchyma (1)
31. Perianth tube well developed (0)—vestigial (1)
32. Outer tepals symmetric about the midvein (0)—asymmetric (2)
33. Tepals uniformly deep blue (0)—tepals pale blue to whitish (1); tepals shades of mauve to turquoise (or cream) (2)

Additional character when Ixioideae is added to matrix

34. Flowers lasting at least one day and not deliquescing on fading (0)—flowers fugaceous, lasting less than a day and deliquescing on fading (1) [scored 0 for *Nivenia* and Ixioideae, 1 for all species of *Aristea*]

[Autapomorphies not included: exine with supratectal verrucae (*A. spiralis*); perigonal nectaries (*A. spiralis*); flower clusters pendent (*A. singularis*); spathes and bracts regularly fringed (*A. africana*); spathes and bracts lacerate (*A. woodi*).]

Table 2. Continued.

Taxon	Character Number						
	12345	1 67890	11111 12345	11112 67890	22222 12345	22223 67890	333 123
Nivpat	00010	00000	000?0	000?0	00000	00000	000
africana	30001	11001	10121	00010	00021	01001	100
anceps	11121	10010	01000	00221	00001	1000?	100
teretifolia	20000	11000	32202	10200	10001	0000?	112
biflora	20000	10000	32202	10200	10001	01001	112
cantharophila	20101	10000	32202	10200	00001	0000?	102
monticola	00020	00011	10011	00100	00101	00101	100
juncifolia	00010	00001	11011	00200	00101	0001?	100
fimbriata	00010	?1001	11??1	00100	00121	010??	100
confusa	00020	00001	11011	00100	00101	0011?	100
dichotoma	30001	11001	10121	00012	00011	0100?	100
ecklonii	11111	10111	21000	00101	00001	00001	100
glauca	30000	11001	10121	00012	00011	0100?	100
lugens	20000	11000	32202	10200	10001	0000?	101
major	00020	00001	10021	00100	01101	0011?	100
spiralis	21120	01000	32202	10201	01001	00001	101
simplex	21111	11000	32202	10200	01001	0000?	101
schizolaena	00120	00001	00000	00200	00001	0000?	100
goetzei	11120	10021	00000	00201	00001	0000?	100
humbertii	11120	100?1	00000	01110	00001	0010?	100
cladocarpa	11121	10011	21000	00101	00001	0000?	100
madagascariensis	11120	10021	00000	01200	00001	0000?	100
kitchingii	11120	10021	00000	01100	00001	0010?	100
angustifolia	11120	10011	00000	00200	00001	0000?	100
nyikensis	11120	10021	00000	00100	00011	0000?	100
ranomafana	11120	10021	00000	01010	00001	0010?	100
polycephala	11120	10021	00000	00010	00011	0000?	100
racemosa	00010	00001	11011	00200	00101	001??	100
pusilla	11121	10110	21000	00101	00001	0000?	100
angolensis	11111	10011	00000	00100	00011	00001	100
oligocephala	30001	11001	10121	00010	00011	0000?	100
platycephala	1112?	10011	20020	00201	00001	0000?	100
abyssinica	11111	10011	00000	00121	00001	1000?	100
singularis	00020	00011	10123	00010	00001	0100?	100
pauciflora	20001	11000	32202	00200	00001	00001	100
woodii	11111	10011	00000	00200	00001	0000?	100
montana	11111	10001	00000	00100	00001	0000?	100
grandis	11120	?0011	00000	00200	00001	0000?	100

retention indices (Figs. 47, 49), are automatically calculated by Hennig86 (Farris, 1988). Because the initial trees were poorly resolved, the successive weighting option was also invoked. Successive weighting, recommended by Farris (1969) for situations where unreliable (homoplasious) characters outnumber reliable ones, is one way to improve tree resolution. The method selectively weights those characters that are more consistent at the expense of those that are homoplasious. The method may be extremely helpful especially when more conventional analyses yield large numbers of trees and consensus trees are poorly resolved. Cladograms were then analyzed using CLADOS (Nixon, 1992) and the trees presented here were generated using this program. We were unable to determine a measure of confidence in the trees obtained by successive weighting by bootstrap analysis (Swofford, 1991) because the number of trees generated using the method was so large in some replicates that it became impractical to perform.

A second series of cladistic analyses was performed after the addition of one more taxon, subfamily Ixioideae, to the matrix. This was because in recent molecular systematic studies using sequences from two chloroplast genes, *rbc*L and *rps*4

(M. Chase et al., 1995, and pers. comm.; Souza-Chies et al., 1997), the subfamily has been found to be nested in Nivenioideae, as a sister clade either to *Nivenia* plus *Witsenia* or *Aristea*. Consequently, we were interested to see how this might affect the topology of the trees.

Results

Palynology

Shape and Size. In hydrated or rehydrated pollen, grains are ellipsoid to nearly spherical. Pollen is typically shed in monads, but in *Aristea ecklonii* and *A. pusilla* the tetrad stage is evidently prolonged, and most pollen is shed as tetrads, a specialized condition (Figs. 1, 2).

Species of *Aristea* fall fairly well into two size classes for pollen-grain size (Table 1). Nineteen of the species examined have medium-sized to moderately large grains (equatorial diameter 45–64 μm) and 13 species have large grains (equatorial diameter more than 69–97.5 μm). *Aristea schizolaena*, with grains 66.7 × 60.0 μm, falls between the two groups. Pollen-grain size among the species examined ranges from a minimum of 45.5 × 42.0 μm in *A. major*, to a maximum of 97.5 × 85.5 μm in *A. oligocephala*, and 97.5 × 93.0 μm in *A. dichotoma*. Species of the outgroup have grains that fall in the medium to moderately large size category (Manning & Goldblatt, 1989), hence this is presumed to be the plesiomorphic condition. Size is correlated with some aspects of Weimarck's (1940) infrageneric classification (Table 1). The four species of section *Aristea* examined all have grains exceeding 80 × 77 μm. The remaining species of that section, *A. recisa*, has grains of comparable size according to measurements given by Schulze (1971a). Only *A. lugens* and *A. teretifolia* (sect. *Pseudaristea*) have comparably large grains. Most other species of section *Pseudaristea* (as redefined by Goldblatt, 1995a) have somewhat smaller grains, more than 71 × 70 μm, and are thus still classified as large according to our definition. Grains of species of section *Racemosae*, excepting *A. fimbriata*, are medium-sized, as are those of sections *Eucapsulares*, *Trilobatae*, *Cladocarpa*, and *Ancipites* (Table 1), including those of the Madagascan species (Goldblatt & Le Thomas, 1992a). Except for *A. schizolaena*, grains of members of these sections have an equatorial diameter less than 65 μm. Pollen grains of the outgroup are less than 65 μm in diameter, hence medium-sized grains are scored 0 and large grains as 1. *Aristea schizolaena*, which has grains intermediate in size between the two size classes, is scored as ?.

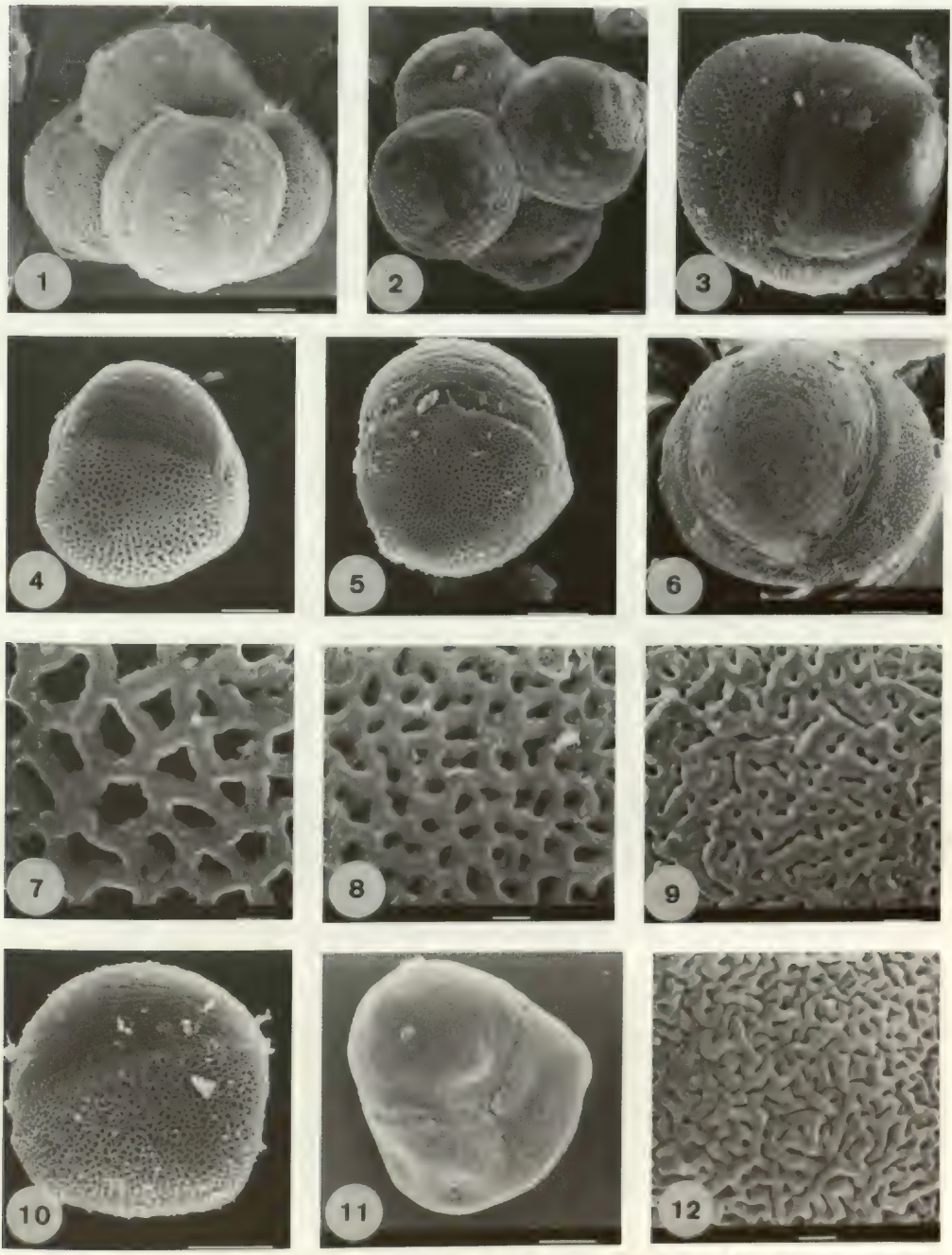
Apertures. Pollen-grain apertures are remarkably variable for a genus the size of *Aristea*. In many cases, correct terminology (sensu Punt et al., 1994) cannot be established because we lack developmental stages necessary for its definition. In our analysis, we recognize four main apertural types. These are treated as four unordered states of one character. The aperture types are as follows.

1. The monosulcate type, which is the plesiomorphic condition for the family based on outgroup comparison (e.g., Goldblatt, 1990). Apertures have been observed in some species at the tetrad stage and determined to be distal, and can reasonably be assumed to be so whenever apertures are unambiguously sulcate (Figs. 3–6, 10, 11). We include in this category the trichotomosulcate aperture of *A. fimbriata* (Fig. 37) because, although the aperture in the species is recognizably different from truly monosulcate apertures, it seems to us to belong in the same general class, being restricted to one face of the pollen grain.

Monosulcate grains are present in five of six species of section *Racemosae* examined (*Aristea confusa, A. juncifolia, A. major, A. monticola, A. racemosa)* and in *A. schizolaena* and *A. singularis*. Among the species examined by Schulze (1971a), *A. macrocarpa* (sect. *Racemosae*) also has monosulcate pollen grains. *Aristea fimbriata*, also section *Racemosae*, alone has trichotomosulculate grains (Fig. 38). As in grains with monosulcate apertures, the aperture is generally wide, reaching the ends of the grain and sometimes extending a short distance onto the non-apertural face. The aperture membrane is typically smooth, that is without substantial amounts of exine on the surface, and the margins are clearly defined. Occasionally tiny fragments of exine are present, visible only using LM (e.g., in *A. fimbriata*).

2. The sulculate type, which includes 1-zonasulculate and disulculate grains, the distinction, in some cases, being difficult to establish because they may occur together in the same species, even in the same sample, and there are often forms intermediate between the two, for example, in species like *A. kitchingii* (Goldblatt & Le Thomas, 1992a) (Figs. 13–24).

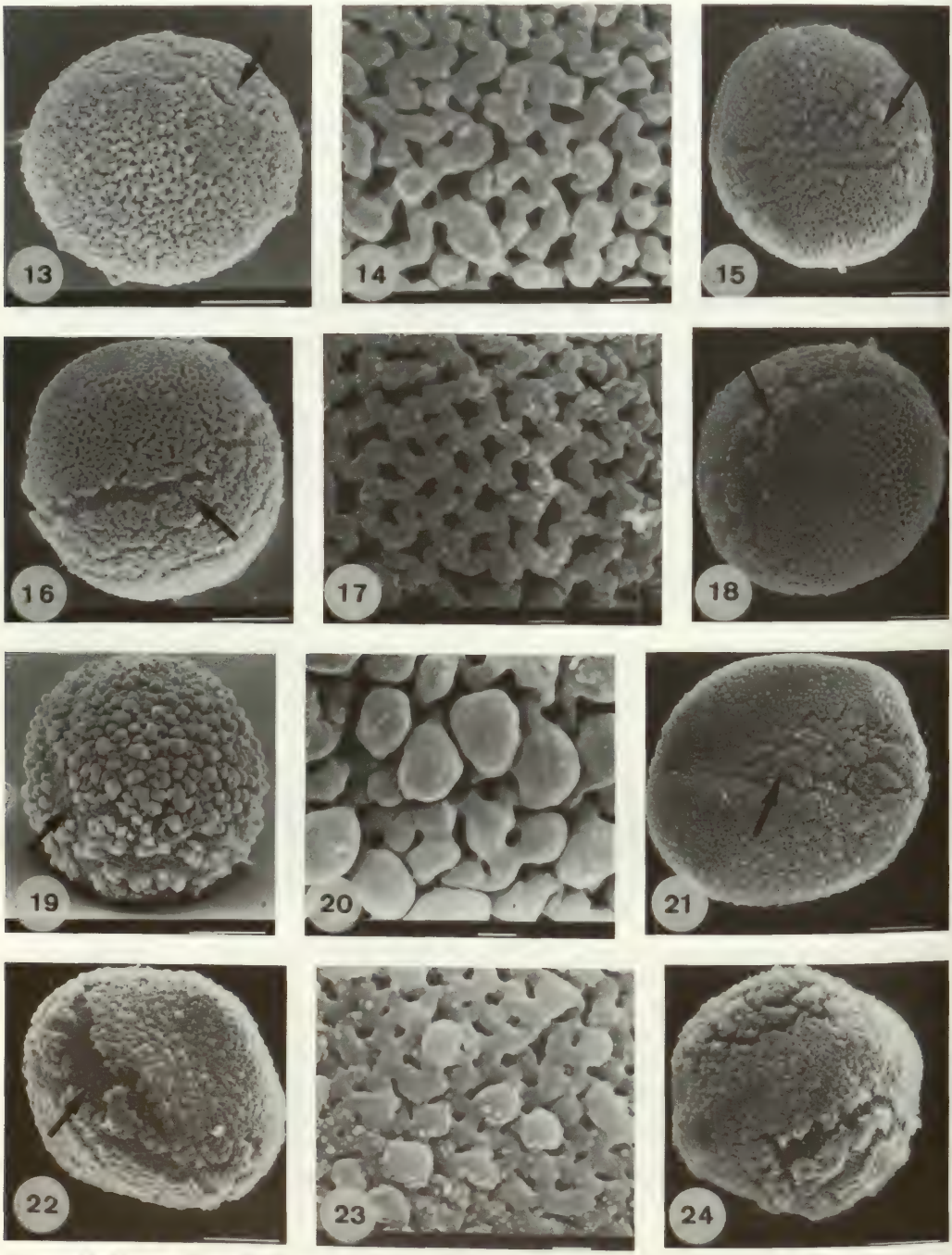
Sulculate grains are the most common type in the genus and are found in 19 species of tropical and eastern southern Africa as well as in 6 of the 7 species that occur in Madagascar. In these grains the aperture is typically obscure and the apertural membrane is covered by more or less disorganized exine, sometimes consisting of an almost complete band, free or not at the ends of the apertures (thus an operculum or pontoperculum) especially in spe-



Figures 1–12. —1. *Aristea ecklonii*: mature grains in tetrads.—2. *Aristea pusilla*: tetrads of mature pollen. 3–12. Monosulcate pollen grains of sections *Racemosae, Singularis,* and *Eucapsulares* with exine detail for selected species.—3. *A. major.*—4 & 7. *A. juncifolia.*—5 & 8. *A. confusa.*—6 & 9. *A. monticola.*—10. *A. schizolaena* (sect. *Eucapsulares*).—11, 12. *Aristea singularis* (sect. *Singularis*). Scale bar: whole grains 10 μm; sculpturing detail 1 μm.

cies (Goldblatt & Le Thomas, 1992a) of Madagascar. The aperture margins are usually diffuse and the ends of the apertures are often difficult to see, apparently sometimes extending around the entire grain (as a zonasulculus—Figs. 13, 15, 19) or interrupted by exine (then evidently disulculate—Fig. 24).

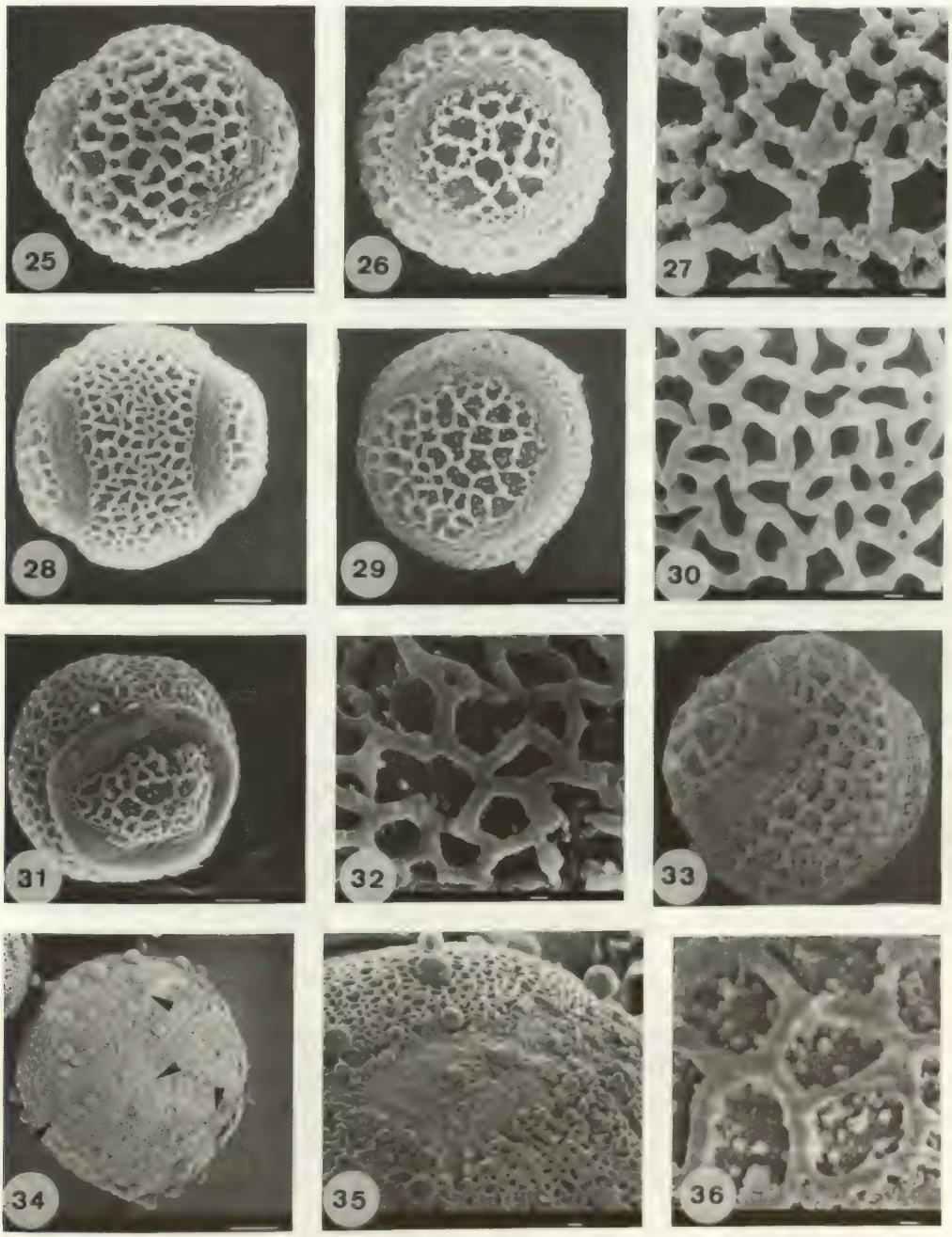
3. The 2-zonasulculate type (Le Thomas &



Figures 13–24. Sulculate pollen grains of section *Eucapsulares* with exine sculpturing in selected species.—13, 14. *Aristea grandis*.—15. *A. angolensis*.—16, 17. *A. montana*.—18. *A. abyssinica*.—19, 20. *A. goetzei*.—21. *A. nyikensis*.—22, 23. *A. ranomafana*.—24. *A. polycephala*. Arrows indicate the apertural zone when not obvious. Scale bar: whole grains 10 μm; sculpturing detail 1 μm.

Goldblatt, 1994; Le Thomas et al., 1996) in which there are two clearly defined zonasulculi (Figs. 25–34), an extremely rare type of pollen grain in flowering plants.

Two-zonasulculate apertures occur in all seven species of section *Pseudaristea* (Table 1). Here, the margins are usually clearly defined (Figs. 26, 29, 31, 34), but in *A. spiralis* (Fig. 35) and *A. pauciflora*



Figures 25–36. Two-zonasulculate pollen grains of section *Pseudaristea* as redefined here, with exine and aperture detail for selected species.—25–27. *Aristea cantharophila*, equatorial and polar view of grains.—28–30. *A. biflora*, equatorial and polar view of grains.—31, 32. *A. lugens*.—33 & 36. *A. teretifolia*.—34, 35. *A. spiralis*, whole grain with arrows pointing to the two zonasulculi, and aperture detail showing diffuse margins, apertural exine fragments, and supratectal exine gemmules. Scale bar: whole grains and apertural detail of *A. spiralis* 10 μm; sculpturing detail 1 μm.

(Le Thomas et al., 1996) they are somewhat diffuse and the apertural membrane is covered with small, scattered fragments of exine. This aperture type is usually constant within a species, but in our sample of *A. simplex*, 2-zonasulculate grains occurred together with some 1-zonasulculate grains. The 1-zonasulculate condition may represent the intermediate phase in the evolution of the 2-zonasul-

culate grain. Pollen of an unidentified plant, apparently closely allied to *A. pauciflora*, but lacking both well-preserved flowers and mature capsules and seeds, has exclusively 1-zonasulculate grains with clearly defined margins and without diffuse exine fragments on the apertural membrane (Fig. 45). These grains recall the 1-zonasulculate grains found in our sample of *A. simplex*. The plant also bears a fair resemblance to *A. zeyheri*, but specimens identified with this species (Weimarck, 1940) clearly belong to section *Racemosae*, close to *A. racemosa*. Like it, they have monosulcate grains (three collections checked under the light microscope). Because of the uncertain identity of the species with these 1-zonasulculate grains, and because so many of its morphological characters are unknown, we were unable to include it in the phylogenetic analysis. This plant, evidently representing an undescribed species, should be investigated in more detail when opportunity arises.

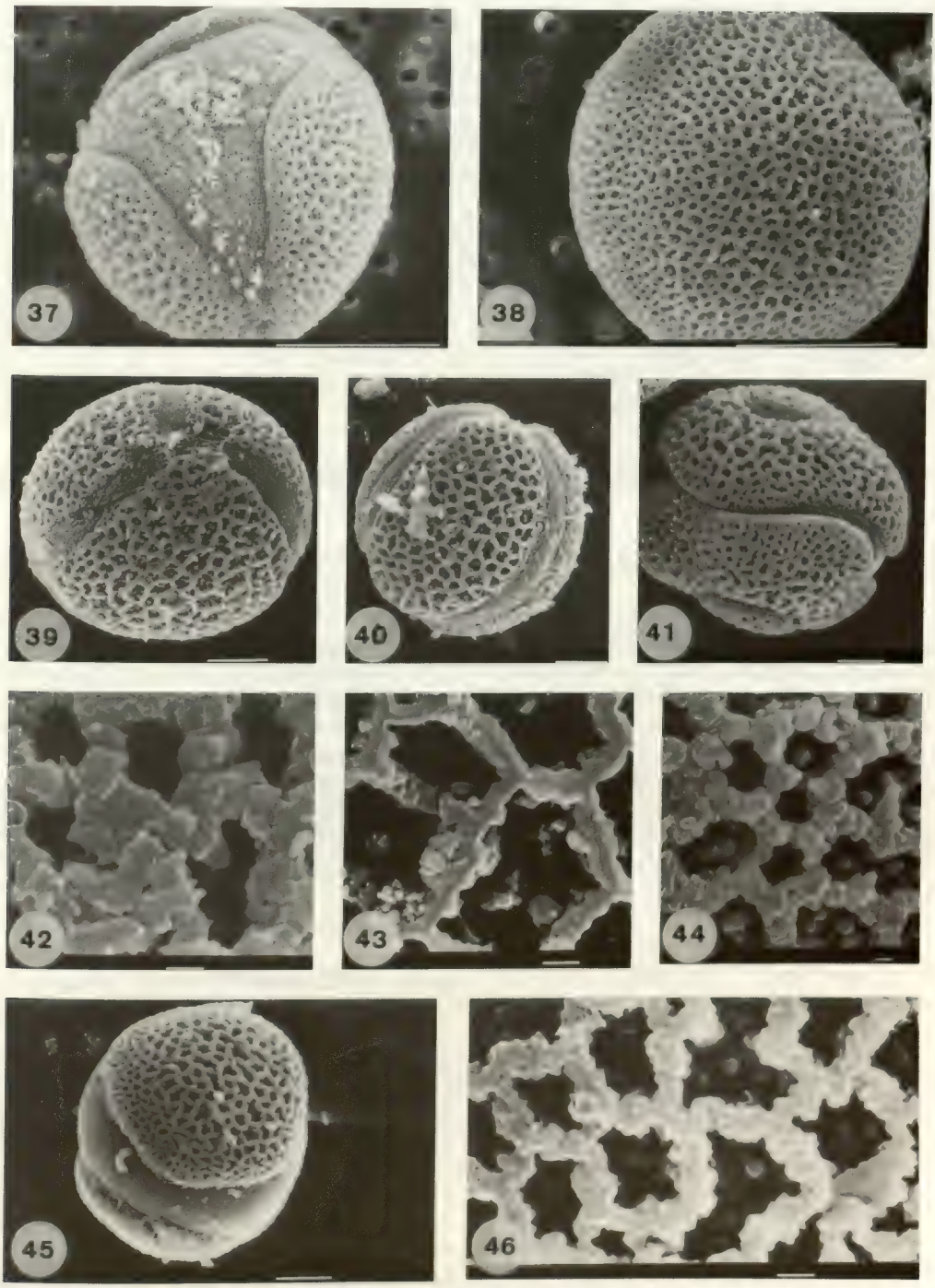
4. The 3-sulcate (or more or less spiraperturate) type (Le Thomas & Goldblatt, 1994; Le Thomas et al., 1996, Goldblatt et al., 1997), known elsewhere in Iridaceae, with well-defined apertural zones separating equal or unequal plates of exine and the sulci always confluent (Figs. 39–41).

Three-sulcate grains are restricted to three of the four species of section *Aristea* examined, and a fifth, *A. recisa*, examined by Schulze (1971a), probably also has this aperture type although it was not specifically so described by him. In *A. oligocephala* of the section, the apertures are difficult to define and are more or less spiraperturate, consisting of several confluent sulci separated by large plates of exine of varying size. The tendency for the spiralization of the aperture apparently corresponds to Schulze's (1971a) observations for the species based on examination of acetolyzed pollen.

In addition to the aperture itself, two more apertural characters are recognized, the nature of the margin and the apertural membrane. Margins are either sharply defined (e.g., Figs. 3–6), the plesiomorphic condition based on outgroup comparison (Manning & Goldblatt, 1989), or diffuse (e.g., Fig. 35). The ancestral condition, again based on outgroup comparison (Goldblatt & Manning, 1989), for the aperture membrane is without fragments of exine (i.e., smooth) (e.g., Figs. 3–5, 39, 40), and in the derived state the membrane is more or less obscured by irregularly shaped, fairly large fragments of exine (e.g., Figs. 13, 15, 16, 21) that sometimes form an operculum-like band (Goldblatt & Le Thomas, 1992a).

Surface sculpturing. The exine is tectate-columellate and the exine patterning ranges from reticulate (Fig. 7, 8, 42–44), to rugulate (Fig. 9, 12), and rugulo-areolate (Fig. 20, 23), depending on the size and shape of the lumina and the orientation of the muri with respect to one another as well as their overall shape. The character states form a continuum and the distinction between them, although clearly defined by terminology (Punt et al., 1994), is arbitrary. The states thus constitute an ordered series of one character. Lumen size is regarded as a separate character from basic exine pattern, and outgroup comparison suggests that lumina of moderate size (1–2 μm in diameter), as for example, in *Aristea confusa* and *A. montana* (Figs. 7, 17), are the plesiomorphic condition for the genus. A reticulum with large lumina (2–6 μm in diameter) characterizes *A. africana*, *A. glauca*, and *A. cantharophila* (e.g., Figs. 27, 42–44), and in these species the bases of the lumina are often prominently verrucate or baculate. Small lumina (less than 1 μm, i.e., microreticulate) characterize *A. juncifolia*, *A. angolensis*, and *A. spiralis*, among others (e.g., Figs. 8, 15, 35). Lumina are normally fairly similar in size, all or most falling in the same size class for a particular sample. *Aristea cantharophila* is, however, exceptional in having mostly large lumina mixed with small lumina on the distal exine plates (Fig. 26). The three states of lumen size are arbitrary divisions of a continuum and intrinsically additive, and the character is treated as ordered.

The exine muri are variable in shape and sculpturing, most often angular and smooth, especially when the lumina of the reticulum are of moderate or small size, but more or less wavy, sculpted, and with perforations when the lumina are large. The species of section *Africana* and some of section *Pseudaristea* are notable for their ridged exine muri (Figs. 27, 42, 44). A remarkable feature of the exine of *A. spiralis* is the presence of large, irregularly distributed, supratectal gemmules on the reticulum (Figs. 34, 35), a condition reported for this species by Radelescu (1970). This recalls the exine of one species of the outgroup, *Witsenia maura* (L.) Thunb., which is autapomorphic in having large verrucae lying on a more or less microreticulate tectum (Manning & Goldblatt, 1989). A typical rugulate sculpturing with more or less elongate exine elements, free or incompletely fused, occurs in *A. monticola* and *A. singularis* (Figs. 9, 12), but in some species in this category the rugulae are contorted, very irregular in shape, and more or less fused (e.g., *A. grandis*—Fig. 14). In this type, the surface of the muri may be smooth or sculpted. All the Madagascan endemic species (Table 3), plus *A. goetzei* and the tropical African endemic *A. nyiken-*



Figures 37–46. 37, 38. Pollen grains of *Aristea fimbriata* (sect. *Racemosae*), section *Aristea* and *A. sp.* (aff. *A. pauciflora*) with exine detail for selected species.—37, 38. *A. fimbriata*, showing apertural and non-apertural surfaces of grains.—39 & 42. *A. africana*.—40 & 43. *A. glauca*.—41 & 44. *A. oligocephala*.—45, 46. *A. sp.* (aff. *pauciflora*). Scale bar: whole grains 10 μm; sculpturing detail 1 μm.

Table 3. Species of *Aristea* with their geographic ranges arranged according to the revised classification proposed here. There are 50 species currently recognized in the genus, one or possibly two undescribed species in section *Racemosae*, and the plant referred to in the text as *G.* sp. *aff. pauciflora* may be an undescribed species of section *Pseudaristea*. Species marked with * are unknown palynologically; those with @ are at least known for the aperture but were not included in the phylogenetic analysis because other pollen characters are unknown. Figures in parentheses are total species in the taxon. The type species of the subgenera and sections are indicated in bold type.

Taxon	Geographical range
Subgenus *Eucapsulares* Goldblatt (24)	
The *A. angolensis* group (= sect. *Aristea* sensu Weimarck) (12)	
A. angolensis Baker (incl. *A. flexicaulis* Baker)	Cameroon and Ethiopia to eastern S. Africa
A. angustifolia Baker	Madagascar
A. compressa Buch. ex Baker*	eastern S. Africa
A. galpinii N. E. Br. ex Weim.*	eastern S. Africa
A. gerrardii Weim.* (closely related to *A. compressa* and possibly not distinct)	eastern S. Africa
A. grandis Weim.	eastern S. Africa
A. montana Baker	eastern S. Africa
A. goetzei Baker (= *A. nitida* Weim.)	Tanzania and Madagascar
A. nyikensis Baker (incl. *A. hockii* de Wild)	southern tropical Africa
A. polycephala Harms	southern tropical Africa
A. schizolaena Harv. ex Baker	eastern S. Africa
A. woodii N. E. Br.	southern tropical and eastern S. Africa
The *A. madagascariensis* group (4)	
A. humbertii H. Perr.	Madagascar
A. kitchingii Baker	Madagascar
A. madagascariensis Baker	Madagascar
A. ranomafana Goldblatt	Madagascar
The *A. ecklonii* group (incl. section *Trilobatae* Weim. and section *Cladocarpae* Weim.) (5)	
A. cladocarpa Baker	Madagascar
A. ecklonii Baker	Cameroon and Uganda to eastern S. Africa
A. ensifolia Muir*	southern Cape Region
A. platycephala Baker	eastern S. Africa
A. pusilla (Thunb.) Ker Gawl.	eastern S. Africa and Cape Region
The *A. anceps* group (= section *Ancipites* Weim.) (3)	
A. abyssinica Pax (incl. *A. cognata* N. E. Br.)	Ethiopia to eastern S. Africa
A. alata Baker*	eastern tropical Africa
A. anceps Ecklon	eastern S. Africa
Subgenus *Pseudaristea* Pax (7)	
A. biflora Weim.	Cape Region
A. cantharophila Goldblatt & J. Manning	Cape Region
A. lugens (L.f.) Weim.	Cape Region
A. pauciflora W. Dod.	Cape Region
A. spiralis (L.f.) Ker Gawl.	Cape Region
A. simplex Weim.	Cape Region
A. teretifolia Goldblatt & J. Manning	Cape Region
Subgenus *Aristea* (21)	
Section *Racemosae* Weim. (13)	
A. bakeri Klatt* (doubtfully distinct from *A. confusa*)	Cape Region
A. confusa Goldblatt	Cape Region
A. cuspidata Schinz*	Cape Region
A. fimbriata Goldblatt & J. Manning	Cape Region
A. inaequalis Goldblatt & J. Manning@	Cape Region
A. juncifolia Baker	Cape Region
A. macrocarpa G. Lewis@	Cape Region

Table 3. Continued.

Taxon	Geographical range
A. major Andrews	Cape Region
A. monticola Goldblatt	Cape Region
A. racemosa Baker	Cape Region
A. rigidifolia G. Lewis*	Cape Region
A. rupicola Goldblatt & J. Manning@	Cape Region
A. zeyheri Baker@	Cape Region
Section *Singulares* Weim. (1)	
A. singularis Weim.	Cape Region
Section *Aristea* (6)	
A. africana (L.) Hoffmsg.	Cape Region
A. dichotoma (Thunb.) Ker Gawl.	Cape Region
A. glauca Klatt	Cape Region
A. oligocephala Baker	Cape Region
A. palustris Schltr.*	Cape Region
A. recisa Klatt@ (closely allied to and perhaps not distinct from *A. africana*)	Cape Region
Uncertain position (Lewis, 1952)	
A. latifolia G. Lewis*	Cape Region

sis (Figs. 20, 21), have a rugulo-areolate sculpturing consisting of very closely aligned rugulae, which sometimes conform to the strict definition of areolae.

In addition to the basic exine patterning we recognize two additional exine characters: surface smooth or sculpted, and with or without perforations. Outgroup comparison indicates that both the smooth condition and the absence of perforations are ancestral.

PHYLOGENY

Preliminary cladistic analyses quickly showed that the data are homoplasious for many characters and that numerous (usually over 1000) trees were obtained whatever option was chosen from the Henning86 package for the analysis. The resulting consensus trees, however poorly resolved, always embodied a number of distinct clades (Fig. 47A). Most notable among them are the clades at nodes 1 and 2 of Figure 47A. Node 1 includes those species of Weimarck's section *Pseudaristea* that have 2-zonasulculate pollen grains combined with elongate capsules, locules deeply lobed longitudinally, and truncated seeds. Node 2 includes Weimarck's sections *Aristea* and *Racemosae* (capsules with prominent narrow wings, radially flattened seeds, and a reduced seed number per locule), plus *A. singularis* (sect. *Singularis*), which has rounded seeds with an aril but winged capsules.

Successive weighting yielded a dramatic reduction in the number of trees and a rise in the consistency index. In the final analysis we obtained just 24 trees that differed minimally, and the strict consensus tree (Fig. 47B) is relatively well resolved. Most significantly, what we call the core species of section *Pseudaristea* (clade 1), also a clade in the unweighted consensus tree, formed a sister clade to the remaining species of the genus (clade 2). The first bifurcation of clade 2 divides its constituent species fairly evenly. Clade 3 of Figure 47B corresponds exactly to clade 2 of the unweighted consensus tree, that is, sections *Aristea, Racemosae,* and *Singularis.* The three sections each constitute a single clade (Fig. 47B, clades 5, 6, and 7). The division corresponds closely to Weimarck's (1940) sectional composition. Clade 3 is supported by fruit and seed characters (winged capsules, radially flattened seeds, few seeds per locule) (Fig. 48).

The poorly resolved sister clade at node 4 includes species of five of Weimarck's sections: all the members of his sections *Eucapsulares* (which he called *Euaristea*) and *Ancipites*; the monotypic sections *Trilobatae* (*A. platycephala*) and *Cladocarpae* (*A. cladocarpa*); and two species of his section *Pseudaristea, A. ecklonii* and *A. pusilla.* There is little support for any large species clusters in clade 4. Notable smaller clades include those at nodes 8, 9, and 10. Clade 8 includes two species of Weimarck's section *Pseudaristea,* plus the single species each of his sections *Cladocarpae* and *Triloba-*

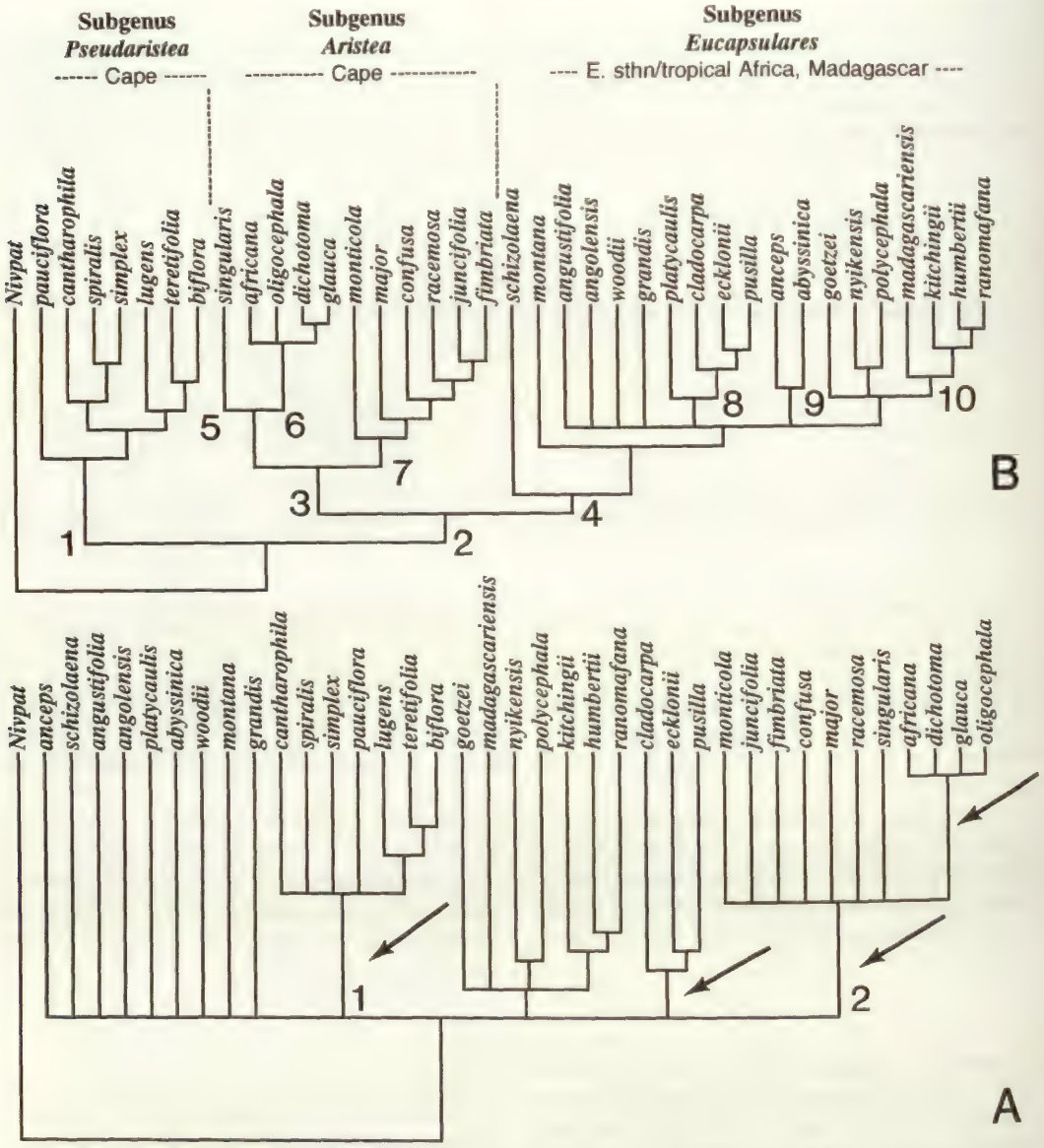


Figure 47. Cladograms showing species relationships in *Aristea* using the matrix in Table 2 with the outgroup *Nivpat*.—A. Strict consensus tree of 1012 equally parsimonious trees obtained using the mh* and bb* options of Hennig86, length (L) 107, consistency index (CI) 45, retention index (RI) 80. Arrows show clades present in all analyses. Clade 1 corresponds to the core species of Weimarck's section *Pseudaristea* and 2, to sections *Aristea*, *Racemosae*, and *Singularis*.—B. Strict consensus tree of 24 equally parsimonious trees (CI 76, RI 93) obtained using the mh* and bb* options of Hennig86 followed by successive weighting (xs w). The three subgenera of the revised classification proposed as a result of the analysis are shown above the main clades. Geographical distribution of the subgenera is also indicated.

tae. Clade 9 includes the two species of section *Ancipites* included in our analysis, and clade 10 has the four Madagascan species with porose anther dehiscence. In the tree selected for plotting characters (Fig. 48), clades 8 and 9 are united (compare with the strict consensus tree, Fig. 47B). The isolated position of *Aristea schizolaena* in clade 4 (Fig. 47B) is difficult to explain in terms of morphology and is discussed below. The topology of the weighted consensus tree produced using the matrix that included the extra taxon, Ixioideae, differs only slightly. In this tree (Fig. 49) Ixioideae falls outside *Aristea* and the three main clades (nodes 1, 2, and 4) are the same as in the analyses without Ixioideae (compare with Fig. 47B). The position of clades 1 and 2 with respect to clade 3 is, however, reversed

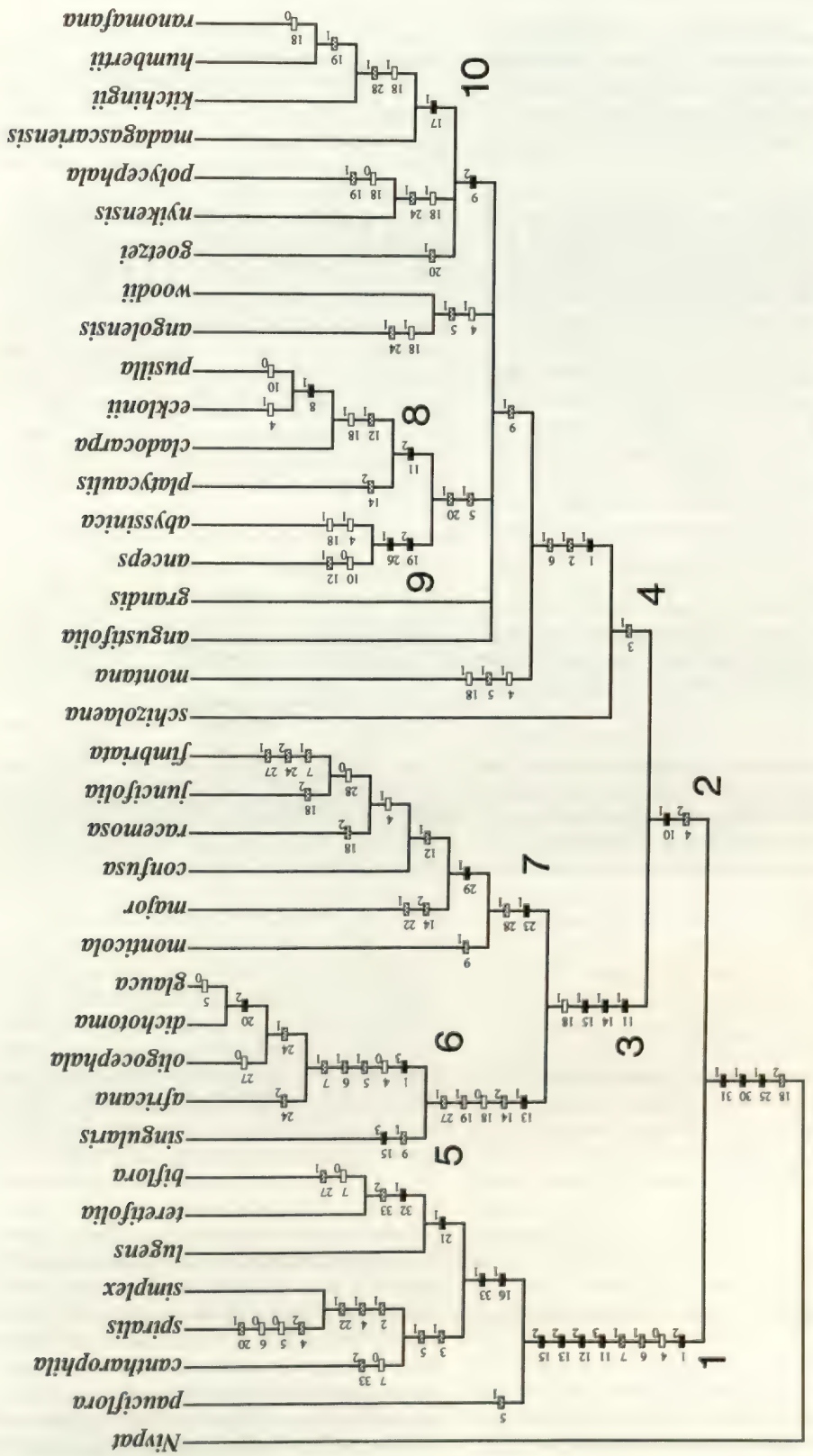


Figure 48. One of 24 trees obtained using the matrix in Table 2 and successive weighting and the mh* and bb* options of Hennig86, showing character distribution (consensus tree shown in Fig. 47B). Numbers opposite the bars on the tree correspond to the character numbers in Table 2; bar shading: solid color = change to the apomorphic state; clear = reversal to the plesiomorphic state (e.g., loss of a specialized condition); stippled = parallel character changes. Taxa were randomly rearranged 15 times with the same result being obtained.

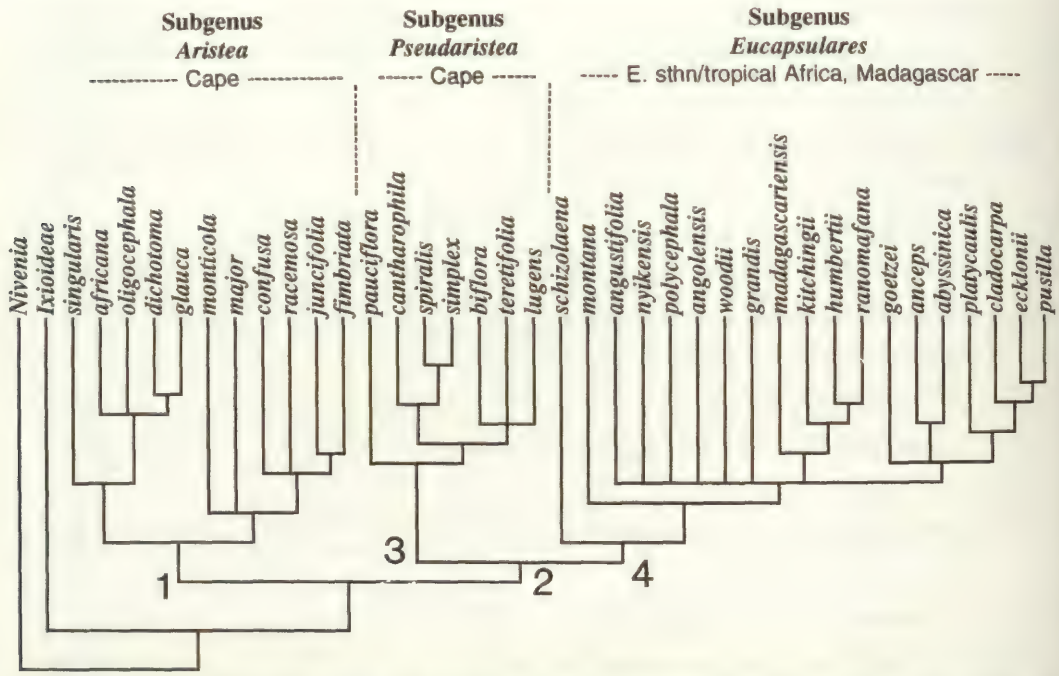


Figure 49. Strict consensus tree of 1012 equally parsimonious trees obtained using the matrix that included the extra taxon, Ixioideae, and using the mh* and bb* options of Hennig86, followed by successive weighting (CI = 45, RI = 80). The same three major clades as in Figure 47B and 48 are present, but the positions of subgenera *Africana* (clade 1) and *Pseudaristea* (clade 2) are shifted in relation to subgenus *Eucapsularis* (clade 3).

compared with their positions in Figures 47B and 48. Within clade 4 of Figure 49 *A. schizolaena* again assumes its isolated position, *A. ecklonii, A. pusilla, A. cladocarpa,* and *A. platycaulis* are a clade, but now link basally to *A. goetzei* and the two species of section *Ancipites.* The four Madagascan species with porose anthers also remain a single clade.

Discussion

Infrageneric Classification

The results of the phylogenetic analysis confirm the monophyly of *Aristea,* assumed in Material and Methods, above. The results also indicate the need for substantial revision of Weimarck's (1940) infrageneric classification. We propose subgeneric status for the three main clades present in the weighted trees we have generated (Fig. 47B, 49). Preserving, where possible, Weimarck's nomenclature, we call these subgenera *Aristea, Eucapsulares,* and *Pseudaristea.* The first of these, clade 3 (Fig. 47B), includes three of Weimarck's sections, *Aristea* (called by him *Cyaneae*) at node 6, *Racemosae* at node 7, and *Singulares* at node 5. The first two are evidently monophyletic and their constitution is supported by the analysis. The third, section *Singulares,* which is monotypic, is nested between these two sections. It does not, as Weimarck assumed, appear to be a taxonomically isolated and primitive member of the genus. As explained elsewhere (Goldblatt, 1995a), the only species of the section, *A. singularis,* was incompletely known to Weimarck and in some respects misunderstood. We hesitate to include *A. singularis* in section *Aristea* (it falls at the base of that clade) because of its odd array of features. It accords with both sections *Aristea* and *Racemosae* in its narrowly winged capsules. The small stature and divaricate inflorescence match section *Aristea,* but the plesiomorphic small pollen grains with monosulcate apertures and apomorphic rugulose exine correspond with section *Racemosae* and contrast starkly with the trisulcate or even more complex grains with reticulate exine of section *Aristea.* On balance, it seems best to maintain section *Singulares.* The unique rounded, and dorsiventrally compressed seeds with a collapsed chalaza, funicular elaiosome, and pendent inflorescence units certainly represent an assemblage of unique features for the genus and support the recognition of a section despite its being monotypic. It is possible that the monosulcate pollen grains represent a reversal to the ancestral state and that *A. singularis* is actually nested in section

Aristea. Elsewhere (Goldblatt, 1995a) the species has been compared to *A. dichotoma*. Future study may throw light on this question.

The second subgenus we recognize (clade 1 of Fig. 47B), subgenus *Pseudaristea*, contains the type and closely related species of Weimarck's section of that name. Two more species of Weimarck's section, *A. ecklonii* and *A. pusilla*, fall in the third subgenus, and *A. zeyheri*, not included in the analysis, is probably a specialized species of section *Racemosae* (Goldblatt & Manning, 1997). These three species were included by Weimarck in section *Pseudaristea* largely on the basis of their elongated capsules. All three have different pollen morphology from the other members of section *Pseudaristea* and differ morphologically in details of capsule morphology. The elongate shape of the capsules, the character used by Weimarck to define his section, must be assumed to be convergent. Including the species described since the publication of Weimarck's monograph, subgenus *Pseudaristea* has just seven species. Their synapomorphies include large pollen grains, extraordinary 2-zonasulculate apertures, exine with a reticulum of very large lumina, on the one hand, and the unique leathery-woody, elongate, tardily dehiscent capsules and cylindrical, truncate seeds combined with long inflorescence spathes on the other.

The third subgenus, *Eucapsulares* (clade 4 of Fig. 47B), incorporates the remaining four sections of Weimarck's classification plus the residue of section *Pseudaristea*, in all some 24 species, 19 of which are included in the cladistic analysis. The species relationships are poorly resolved and our results do not support the recognition of any formal taxonomic groupings within the subgenus. Instead, we suggest using an informal solution, referring simply to "species groups" for well-defined clades. One of these is particularly noteworthy. *Aristea ecklonii* and *A. pusilla* are linked to the Madagascan species *A. cladocarpa* (sole species of sect. *Cladocarpa*) and then to *A. platycephala* (sole species of sect. *Trilobatae*). The latter, an eastern South African endemic, was assigned its own tribe by Weimarck because of its distinctive short, warty capsules. It is otherwise fairly similar to *A. ecklonii* morphologically, and its position on the same clade is not surprising. We suspect that one more species, the southern Cape *A. ensifolia*, which is confined to forested habitats, will fall in this clade too, but pollen is so far unavailable and the species could not be included in the phylogenetic analysis. *Aristea ensifolia* also has elongated capsules, but they are unusual in being indehiscent. The relatively soft capsule walls simply decay with age, gradually releasing the seeds around the parent plants.

A second small clade, the *Aristea anceps* group, includes the two species of Weimarck's section *Ancipites*, *A. abyssinica* and *A. anceps* (a third, *A. alata*, will probably also fall here). A common synapomorphy with the *A. ecklonii* group, compressed and broadly winged stems, is the reason the two groups are linked in Figure 49 in a single clade.

Another clade that appears in the successively weighted trees of both analyses, the *A. madagascariensis* group, includes the four Madagascan species that have apically dehiscent anthers, *A. humbertii*, *A. kitchingii*, *A. madagascariensis*, and *A. ranomafana* (Goldblatt, 1991, 1995b). The remaining species of Weimarck's section *Eucapsulares* exhibit little evidence of relationship. Species not included in our analysis, *A. compressa* and *A. gerrardii*, appear to us to be fairly closely allied to *A. angolensis*, and we are confident that they would fall close to this species in phylogenetic analyses.

The isolated position of *Aristea schizolaena* in subgenus *Eucapsulares* is difficult to explain in terms of morphology. The species is sister to the remainder of the *Eucapsulares* clade, and its basal position is the result of its having plesiomorphic pollen grains the sulcate apertures of which are smooth. The remaining species have sulculate pollen grains with more complex apertures (disulculate or zonasulculate) always covered with irregularly shaped exine masses. The apparently plesiomorphic pollen grains may represent a reversal, but an alternative position for *A. schizolaena* would result in longer (less parsimonious) trees. The remaining species of the subgenus have sulculate pollen grains, with more complex apertures covered with irregularly shaped exine masses. Morphologically, *A. schizolaena* is unexceptional. It appears to be closely related to the eastern southern African *A. grandis*, *A. montana*, and *A. woodii* and is readily confused with *A. woodii*. We are reluctant to ascribe any taxonomic significance to the basal position of the species.

The remaining species of subgenus *Eucapsulares* form a residual group that includes the type species of section *Eucapsulares*, *A. angolensis*. We suggest referring to these species as the *A. angolensis* group.

PHYTOGEOGRAPHY AND PHYLOGENY

There is an extremely close correlation between the phylogeny (and the revised classification based on the phylogeny) and geographical distribution (Fig. 50). All three sections of subgenus *Aristea* oc-

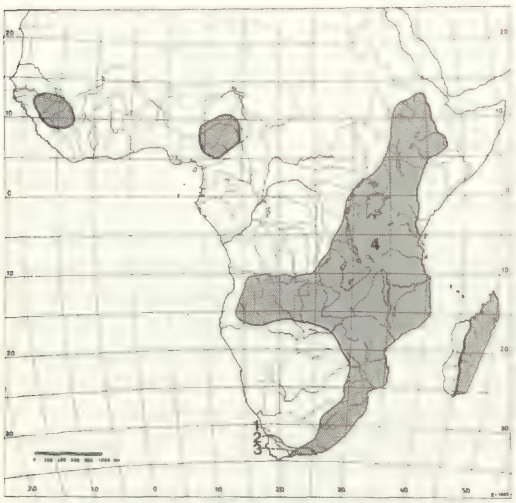


Figure 50. Africa and Madagascar showing the distribution of infrageneric taxa of *Aristea*.—1. Section *Aristea* of subgenus *Aristea*.—2. Section *Racemosae* of subgenus *Aristea*.—3. Subgenus *Pseudaristea*.—4. Subgenus *Eucapsulares*. The Cape Floristic Region nearly corresponds to the range of section *Racemosae* (2).

cur in the winter rainfall climate zone of southern Africa, the Cape Floristic Region (Bond & Goldblatt, 1984) and southern Namaqualand to the north, a part of the Greater Cape Flora Region. With the exception of one species (or two, depending on taxonomy), members of the subgenus are actually restricted to the southwest of the region. Only *A. confusa* and *A. bakeri* (if that species is separate from *A. confusa*) extend eastward to abut the main range of subgenus *Eucapsulares*.

All the species of section *Pseudaristea* also occur in the southern African winter-rainfall zone, thus within the Cape Floristic Region proper. Again, species concentration is highest in the west, repeating the pattern in sections *Aristea* and *Racemosae* of subgenus *Aristea*.

The geographical distribution of subgenus *Eucapsulares* is far wider, extending across all of sub-Saharan Africa and Madagascar. Species diversity exhibits a pattern fairly typical for predominantly temperate-adapted taxa of fewer species as one moves equatorward. There are 14 species of the section in the southern African summer-rainfall zone (including Lesotho, southern Mozambique, eastern South Africa, and Swaziland), of which seven are endemic there. Seven species occur in the Flora Zambesiaca Region (including Malawi, northern Mozambique, Zambia, and Zimbabwe) plus southeastern Zaire. Species endemic to this region plus adjacent southwestern Tanzania include *A. nyikensis* and *A. polycephala*. There are eight species in East Africa-Ethiopia, of which *A. alata* is endemic to the wetter highlands of Kenya, northern Tanzania, and southern Ethiopia. A second species, *A. goetzei*, until recently thought to be endemic to Tanzania, is now considered conspecific with the Madagascan *A. nitida*, a later name (Goldblatt, 1996a). Just three species occur in West Africa, none endemic there (unless *A. djalonis* A. Chev. ined., currently included in *A. angolensis*, is recognized). Distribution patterns of more widespread mainland tropical African species of *Aristea* are also informative. The non-endemic species of each of the broad tropical African regions circumscribed above are shared with southern Africa or, in the case of *A. goetzei* with Madagascar, and never with the adjacent region of tropical Africa alone. Thus, *A. abyssinica* and *A. ecklonii* both extend from the contact zone between the South African summer- and winter-rainfall zones northward to Ethiopia and with isolated populations in the highlands of Cameroon. *Aristea angolensis* has a somewhat wider range, extending from eastern southern Africa to Ethiopia in the north and Senegal in West Africa.

Madagascar has seven species of *Aristea*, six of which are endemic. Only *A. goetzei* is shared with southwestern Tanzania. These endemics include species of at least two clades and possibly three (the phylogenetic position of *A. angustifolia* is uncertain). Thus it appears that *Aristea* has colonized Madagascar at least three times from ancestral stock on the African mainland, a notable departure from the usual pattern of African Iridaceae, which are otherwise poorly represented on that island (Goldblatt, 1991, 1994).

BIOLOGY AND ADAPTIVE RADIATION

About the remarkable diversity of pollen types in *Aristea* very little can be said, and nothing conclusive. Pollen variability does not seem to be correlated with any aspect of floral ecology or habitat. Floral presentation in *Aristea* is remarkably uniform. Except for microscopic details of the style branches, flowers of most species seem to be for all intents and purposes identical. The similarity extends even to phenology. Flowers typically open shortly after sunrise and collapse and deliquesce in the early afternoon. Pollination of species with these flowers is, as far as known (Goldblatt & Manning, 1997), by pollen-collecting female bees of the families Anthophoridae, Halictidae, and as is often the case in Africa, *Apis mellifera* (Apidae).

The only exceptions to this pattern are three (possibly five) species of section *Pseudaristea* that appear to be adapted for pollination by beetles

(Scarabaeidae: Rutilinae: Hopliinae), a strategy evidently unique to the winter-rainfall region of southern Africa (Goldblatt & Manning, 1996 and unpublished). These species have flowers that open in mid morning, last until late afternoon, and are pale blue, mauve, or cream with dark contrasting markings. One additional species of the section, *A. spiralis*, is pollinated by long-tongued flies (*Philoliche*: Tabanidae) (Johnson, 1992; Goldblatt & Manning, 1997), but at least *A. pauciflora* of the section has the plesiomorphic pollination syndrome of the genus (Goldblatt & Manning, 1997). Yet all species of the section have virtually the same type of specialized pollen.

We surmise that climate may be a factor with regard to pollen aperture in the section. The winter-rainfall and summer-dry climate is one that is particularly stressful to plants, many of which flower after the wet season and when atmospheric aridity is high and desiccating winds frequent. Drying of delicate floral parts including stigmatic surfaces and pollen grains may put reproductive success at risk. Pollen grains with germination grooves or pores not restricted to one surface of the grain may be an adaptive advantage under such circumstances, once they are transported to a receptive stigma. Two-zonasulculate, trisulcate, or spiraperturate grains like those of sections *Africana* and *Pseudaristea* are more likely to have an aperture in direct contact with the moist stigmatic surface than monosulcate grains with the aperture restricted to one surface. Perhaps it is no accident that the most peculiar pollen grains in *Aristea*, if not in the entire Iridaceae, occur in species restricted to this particular climate zone. In this respect we note that the subfamily of Iridaceae that has radiated most prominently in this region also has unusual pollen for the family, the monosulcate aperture almost invariably having an operculum (Goldblatt et al., 1991).

It must be noted, however, that not all the species of the southern African winter-rainfall region have specialized pollen grains. Apparently plesiomorphic grains characterize all the species of sections *Racemosae* and *Singulares*, and this pollen type is barely represented in the genus outside the winter-rainfall region. In regard to the peculiar sulculate grains with the apertures largely obscured by exine fragments that characterize species of section *Eucapsulares*, we can offer no suggestion of its adaptive value.

Unusual floral features such as tepal markings and elongate anthers, restricted to some species of section *Pseudaristea* (e.g., *A. biflora, A. cantharophila, A. lugens, A. teretifolia*), are evidently directly related to their pollination system. Hopliine beetles are attracted to dark markings on a pale background, and although they are successful pollinators, they also forage on pollen. The larger anthers of species of the section evidently compensate for some loss in pollen by the production of more grains. In *A. spiralis* secretion of nectar and its particularly long stamens are similarly a direct adaptation to a pollination strategy, in this case to long-tongued fly pollination. The flies are nectar feeders, and the long filaments are necessary to permit placement of the pollen-bearing anthers sufficiently distant from the nectar source that they brush against a foraging insect's body as it feeds.

Variation in capsule and seed morphology, so conspicuous in *Aristea*, seems more amenable to evolutionary speculation. High wind velocities are common in the southern Africa winter-rainfall zone at the time when capsules ripen, exposing the seeds. Flattened seeds are more likely than small rounded or angular ones to offer sufficient wind-resistance to be blown some distance away from the parent plant. We suggest that the flattened seeds of species of subgenus *Aristea* are simply adapted for wind dispersal. In the case of *A. singularis* of the subgenus, the rounded seeds with an elaiosome must be dispersed by ants, a strategy well known in the winter-rainfall zone of southern Africa (Bond & Slingsby, 1983; Linder, 1985). We assume that this is a novel adaptation in a subgenus in which the flattened seeds are evidently adapted to wind dispersal. *Aristea singularis* grows in rather sheltered sites such as in the lee of rocks and in shade where wind dispersal is unlikely to operate effectively.

The elongate, leathery-woody, tardily dehiscent capsules of section *Pseudaristea* suggest another strategy for survival in the southern African winter-rainfall zone. Flowering occurs from September to November in the various species, but the seeds are not shed for at least six months after ripening and thus are held in the hard-walled capsules until the rainy season, which begins in April or May. The capsules decay under wet conditions and then release their seeds at a time most favorable for germination. The tough capsules presumably serve as protection from both desiccation and insect predation during the long period that the seeds are retained.

We suggest that these alternative strategies for survival, seed dispersal and/or pollination in different lineages explain to some extent the peculiar adaptations of pollen apertures, flower coloring, anther enlargement, and seed morphology that have permitted species in different lineages of *Aristea* to survive and radiate in the comparatively hostile en-

vironment in the southern African winter-rainfall zone. In this tiny area, less than 1% of the entire range of the genus, there are 28 species of *Aristea* (25 of them endemic), belonging to two subgenera, one with three sections. The only species of the remaining subgenus, *Eucapsulares,* that occur in the winter-rainfall zone are *A. ensifolia* and *A. pusilla.* Both occur in the more mesic southern part of this zone, the former restricted to moist forest or streamside habitats.

Radiation of subgenus *Eucapsulares* clearly follows highland areas in both southern and tropical Africa as well as Madagascar, where it is restricted to areas of relatively high rainfall. The species do not exhibit any particularly striking adaptations in their reproductive morphology. Elongated capsules are restricted to some species of forest or forest margin habitats. It is not clear why the production of more seeds per capsule should occur in this habitat. Eastern southern African and tropical African species show very discrete habitat preferences. Open grassland, short grassland, marshland, and forest each harbor particular species. Except for some species of forested habitats that have elongate capsules, there appear to be no gross morphological or reproductive correlates. Radiation in subgenus *Eucapsulares* thus appears largely habitat-driven.

To put the above observations in perspective, we restate the extraordinary degree of variation in pollen characters in this genus of only moderate size. This variation equals or even exceeds the range of variation found across all the remaining ca. 1700 species of Iridaceae. Much larger genera, including *Gladiolus* (ca. 255 species) and *Moraea* (ca. 130 species), for example, are constant for aperture type and show limited size and exine sculpturing variation (Schulze, 1971a; Goldblatt, 1996b; Goldblatt et al., 1991; Goldblatt & Le Thomas, 1992b). Only *Iris* (ca. 220 species) comes close to *Aristea* in having a range of aperture types and moderate variation in exine patterning (Schulze, 1971b). Why pollen should be so variable in *Aristea* remains ultimately puzzling. Part of the reason may lie in the geological age of the genus. We suspect that it is one of the oldest genera of the family, most likely of pre-Tertiary age. Time alone may have allowed variation in pollen apertures and exine patterning to accumulate, and ultimately to be selected for during periods of climate change such as the establishment during the Pliocene of semiarid and ultimately Mediterranean climate at the southwestern extremity of the African continent.

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APPENDIX 1. Discussion of morphological characters and their polarization and division into character states. Numbers refer to sequence of the character in the matrix.

1–9. Discussed fully in main text.

10. Prominent rhipidial spathes that enclose the entire inflorescence including the floral bracts, the ancestral state, characterize all genera of the outgroup excepting a few specialized species of *Nivenia*. Within *Aristea* most species have short rhipidial spathes that partially enclose the inflorescences so that the buds and floral bracts are not concealed, the derived state. The floral bracts are usually as long as or longer than the spathes in these species. The exception: species of section *Pseudaristea* have large rhipidial spathes that exceed the floral bracts and conceal the buds.

11. Capsules of the outgroup are rounded in section or barely three-lobed. Derived broadly winged capsules (sects. *Aristea* and *Racemosae*) are scored as 1 and deeply 3-lobed capsules (sect. *Pseudaristea* and a few species of section *Eucapsulares*) are scored as 2. The states are regarded as unordered.

12. Capsule shape in profile is treated as a separate character from shape in transverse section (character 11). Most species of the outgroup have capsules more or less ovoid and up to twice as long as wide. [The elongate, fusiform capsules of one genus of the outgroup, *Patersonia*, are probably specialized owing to their inclusion in the spathes.] Oblong capsules 3–4 times as long as wide are scored as 1, and extremely elongate capsules more than 5 times as long as wide (all species of sect. *Racemosae*) are scored as 2. The character states are additive and hence treated as ordered.

13. Capsules are cartilaginous to nearly woody and loculicidally dehiscent for at least one-third their length in the outgroup genera as well as in most species of section *Eucapsulares*. Capsules of section *Aristea* are cartilaginous with particularly thin lateral walls of the wings and dehiscent only near the apices and often partially along the septa as well. These capsules are scored as 1. Capsules are incompletely known in *A. singularis* but appear to conform to type 1 and are so scored. Species of section *Pseudaristea* have leathery to woody, tardily dehiscent to indehiscent capsules, scored 2. The character states are treated as unordered.

14. Seed number is largely independent of capsule length. Seed number per locule is few (usually one) in the outgroup genera *Klattia*, *Nivenia*, and *Witsenia* but several to many in *Patersonia*. We score the outgroup as ? for this character. Most species of *Aristea* have several to many seeds per locule. Several species of section *Racemosae* typically have four seeds per locule, scored 1, and some have two (or one) per locule, as do all species of section *Aristea*, scored 2. The states are additive and treated as ordered.

15. Rounded to segmental (prismatic) seeds are the most common type in *Aristea* and in the entire family. *Patersonia* has seeds of the same type, scored as 0, but *Klattia*, *Nivenia*, and *Witsenia* have tangentially flattened, shield-shaped seeds, unique in Iridaceae (Manning & Goldblatt, 1991). Radially compressed seeds characterize sections *Aristea* and *Racemosae*, scored as 1. The more or less cylindric seeds with truncated or oblique ends are scored as 2, and the globose, vertically compressed, arillate seeds of *A. singularis* are scored 3. The character states of seed shape are treated as unordered.

16. Anthers are relatively short and oblong in the outgroup genera and most species of *Aristea* as well. Species of section *Pseudaristea*, except *A. pauciflora*, have linear anthers, regarded as derived.

17. Longitudinal anther dehiscence is plesiomorphic in Iridaceae and is the usual condition in *Aristea*. Four Madagascan species have apomorphic apically dehiscent anthers (Goldblatt, 1991, 1995b).

18. When flowering stems have more than just one terminal inflorescence the lateral inflorescences are borne on short branches (or occasionally long branches in the outgroup). In some species of *Aristea* at least a few of the lateral inflorescences are sessile, and sometimes the normal condition is for all lateral inflorescences to be sessile.

It seems useful to distinguish two states, some lateral inflorescences consistently sessile (1), or all normally sessile (2). The character is additive and hence is regarded as ordered.

19. The arrangement of individual inflorescence units is highly variable in Nivenioideae. The ancestral condition is most likely racemose (Goldblatt, 1993), with lateral inflorescences borne on short lateral branches (sessile lateral branches, thus spicately arranged, are considered homologous). Species of section *Aristea* have the inflorescences arranged dichotomously, scored 1. *Aristea abyssinica* and *A. anceps* have one or two inflorescence units crowded at the stem apex, scored 2. The character states are unordered.

20. The outgroup genera have lightly compressed or terete flowering stems, and this is the condition in most species of *Aristea*. A few isolated species have strongly compressed, more or less two-winged flowering stems (ancipitous sensu Weimarck, 1940), including *A. spiralis* (sect. *Pseudaristea*) and *A. abyssinica, A. alata, A. anceps, A. cladocarpa,* and *A. platycephala* (sects. *Ancipites, Cladocarpae,* and *Trilobatae* of Weimarck). In *A. dichotoma* and *A. glauca* the upper part of the flowering stem is also compressed, but the stems are narrow and only obscurely winged. The two states are scored as 1 and 2, respectively, and are treated as unordered.

21. Most species of *Aristea* as well as those of the outgroup genera have the inner tepal whorl similar to the outer in length and color (flowers of *Patersonia* have very short to vestigial inner tepals, clearly apomorphic for that genus). Only *A. lugens* and *A. teretifolia* have the outer tepals substantially smaller than the inner and differently colored.

22. Flowers are more or less upright in the outgroup and all but two species of *Aristea*. Only *A. simplex* and *A. spiralis* have secund flowers that face to the side.

23. Styles of Nivenioideae range from minutely notched apically, broadly lobed apically, or divided into slender recurved arms. The pattern in the outgroup is confusing and we prefer to score the outgroup as ?. In *Aristea* most species have lobed and fringed style branches, scored 0, and a few species, all section *Racemosae,* have the styles minutely notched apically, scored 1.

24. The rhipidial spathes, and usually the floral bracts, are green to brownish and chartaceous in the outgroup. A few species of *Aristea* have the spathes and bracts pale, scarious and either semitransparent, scored 1, or opaque, scored 2 (Table 2). The character states are regarded as unordered.

25. Septal nectaries are present in all genera of the outgroup (Goldblatt, 1993; Rudall, pers. comm.). Species of *Aristea* do not produce nectar, thus lack nectaries, except for *A. spiralis,* which has perigonal nectaries (J. C. Manning, pers. comm.). Absence of nectaries is regarded as derived.

26. The ancestral condition in Iridaceae, including nearly all species of *Aristea,* is a flowering stem bearing a few leaves decreasing in size above. A few species, including *A. abyssinica* and *A. anceps* (Table 2), have a flowering stem consisting of one long basal internode and bearing a short subterminal bract-like leaf.

27. A low, cushion-like growth form is rare in Iridaceae and not present in the genera of the outgroup. Species of section *Aristea* and *A. singularis* may be described as forming low, cushion-like tufts with the flowering stems often not raised much above the leaves.

28. Few to several inflorescence units (or only one) per flowering stem are plesiomorphic in the outgroup genera. Stems with many inflorescence units are a conspicuous feature of a few species (Table 2), notably *A. major* and *A. confusa* (sect. *Racemosae*).

29. Seed surfaces in the outgroup genera typically have primary sculpturing (Manning & Goldblatt, 1991), as do most species of *Aristea,* the surface usually being more or less rugose (unpublished data), treated as the plesiomorphic condition. Seeds of species of section *Racemosae* examined (Table 2) lack primary sculpturing and are treated as derived.

30. Species of the outgroup have leaves with a strand of sclerenchyma below the margins (Rudall & Burns, 1989), but all species of *Aristea* examined for the character lack subepidermal marginal sclerenchyma (Rudall, 1995; J. Manning, pers. comm.), regarded as a derived condition (0).

31. A perianth tube is present in all genera of the outgroup and is presumably plesiomorphic for Nivenioideae. All species of *Aristea* have the tepals united basally in a vestigial tube, 1–2 mm long, scored as 1.

32. Tepals of the outgroup and most members of the ingroup have tepals symmetric about the midvein. The inner tepals are conspicuously asymmetric about the midvein in *A. biflora* and *A. teretifolia,* thus apomorphic for tepal symmetry.

33. The ancestral flower color in Nivenioideae is most probably blue (present in all *Nivenia,* all but one species of *Patersonia,* most species of *Aristea*). A few species of subgenus *Pseudaristea* have pale blue flowers, but three species have cream to mauve flowers (Table 1). Flower color is treated as an unordered multistate character, blue (0), pale blue (1), mauve to cream (2).

Additional character when Ixioideae is included in the analysis:

34. Flowers lasting at least one day and not deliquescing on fading characterize *Klattia, Nivenia, Witsenia,* and all Ixioideae. Flowers of *Aristea* last less than one day (usually fading just after midday) and deliquesce on fading, the derived state.

CHROMOSOME CYTOLOGY OF IRIDACEAE—PATTERNS OF VARIATION, DETERMINATION OF ANCESTRAL BASE NUMBERS, AND MODES OF KARYOTYPE CHANGE[1]

Peter Goldblatt[2] *and Masahiro Takei*[3]

ABSTRACT

Against a background of 100 original counts for 95 species in 34 genera of Iridaceae, we review chromosome information for the entire family. Counts are now available for some 1008 of the estimated 1750 species of Iridaceae, and all but 5 of ca. 78 genera are known from at least one count. We suggest ancestral base numbers for all genera known cytologically and outline patterns of cytological variation within the subfamilies and tribes currently recognized. Polyploidy was evidently important in the early diversification of Iridaceae, and many genera have base numbers higher than $x = 10$. Neopolyploidy is important in Northern Hemisphere genera, especially *Iris* and *Crocus*, but has an unusually low frequency in Africa, the center of diversity for the family. Changes in basic number, frequent in a few genera, are evidently the result of dysploid reduction. In all but a few possible examples, correlated morphological specialization suggests that dysploid reduction is involved in stepwise change in base number. Major dysploid series are restricted to a few genera, including *Romulea*, the related *Crocus*, as well as *Gladiolus* and *Lapeirousia* (all Ixioideae), and *Iris*, *Moraea*, and *Sisyrinchium* (Iridoideae). All other genera have a single base number or limited variation evident in only one or two species. Patterns of chromosomal variation are particularly complex in *Iris* and *Crocus* and await detailed elucidation. More counts are needed in the Australian *Patersonia*, the South American-Australasian *Orthrosanthus*, and the neotropical tribe Mariceae, for all of which ancestral base number remains uncertain and patterns of cytological variation appear complex.

Chromosome cytology in the petaloid monocot family Iridaceae is unusually varied in features of the karyotype including basic number, ploidy level, overall size, and chromosome arm ratios. It is thus an important factor in considerations of the systematics and evolution of this family of some 1750 species in ca. 78 genera (Goldblatt, 1990a, 1991). Iridaceae are consequently comparatively well known chromosomally. Including several new counts published here for a range of genera and species, some until now poorly or not at all known cytologically, there are now counts available for at least half the species in the family, including a good sampling of three of the four subfamilies currently recognized: Nivenioideae, Iridoideae, and Ixioideae. The fourth subfamily, Isophysidoideae, which is monotypic, remains uncounted, an unfortunate gap in our knowledge because this taxon appears to occupy a basal or near basal position in the family (Goldblatt, 1990a; Chase et al., 1995 and unpublished). Ancestral chromosome numbers can be suggested for almost all genera, and patterns of chromosomal variation within genera, and sometimes among related genera, now seem to be reasonably well understood.

Here, patterns of chromosomal variation are interpreted against a background of the systematics and morphology of the Iridaceae. We also draw attention to those genera that are uncounted or poorly known and require further investigation in order to interpret the variation in their karyology. As part of our review of chromosome number and morphology of the family, we also review the available data on genome size.

Methods used are described elsewhere (Goldblatt, 1990a; Goldblatt et al., 1993; Goldblatt & Takei, 1993) and invariably involved squashes of root tips or shoot apices, pretreated in a variety of ways.

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[2] B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

[3] Biological Institute, Oita University, Oita 870–11, Japan.

Results

Original counts are presented in Table 1, accompanied by voucher information. Karyotypes are not described individually; instead, results are illustrated and notable karyotypic details are described under Discussion.

Discussion

Patterns of Variation and Determination of Ancestral Base Numbers

1. Nivenioideae

This relatively primitive subfamily of six genera and ca. 85 species (Table 2) consists of the large African and Madagascan *Aristea*, the Madagascan saprophyte, *Geosiris*, three shrubby southern African genera, and the Australasian *Patersonia*. Derived features of the subfamily (Manning & Goldblatt, 1991) are a binate rhipidial inflorescence, a blue perianth that is fugacious and deliquescent in some genera, and a 2–3-seriate outer seed integument. *Aristea* and the shrubby southern African *Klattia*, *Nivenia*, and *Witsenia* have a common base number, $x = 16$ (Table 2), and small chromosomes (Figs. 1–5) with a size range 0.8–2.5 μm. *Patersonia* is inadequately sampled (Goldblatt, 1979a) and also has small chromosomes (Fig. 6), comparable in size to those of *Aristea*. Diploid numbers of $2n = 62$, 42, and 22, the latter the most frequent, have been reported in the 6 species of *Patersonia* counted out of a total of 20 in the genus. From these counts we assume the most likely ancestral base number for *Patersonia* may be $x = 11$. It seems premature to speculate about how the base number in *Patersonia* relates to $x = 16$ in the remaining genera of Nivenioideae. *Patersonia* has been suggested to be nested within Nivenioideae and to be the sister genus to the lineage that includes *Nivenia*, *Klattia*, and *Witsenia* (Manning & Goldblatt, 1991). If $x = 11$ is correct, then ancestral base number in *Patersonia* must be derived. Additional counts in the genus are needed before the situation here is clarified. *Geosiris* is unknown cytologically.

2. Iridoideae

Iridoideae share with Ixioideae specialized xylem vessels in the roots with simple perforations, likely a specialized condition (Cheadle, 1963; Goldblatt et al., 1987), similar and putatively derived anther endothecial thickenings (Manning & Goldblatt, 1990), and a more specialized spectrum of flavonoid compounds than in Nivenioideae (Goldblatt, 1990a). Possibly a clade, Ixioideae and Iridoideae, nevertheless, differ considerably in many features, including pollen grain morphology, leaf anatomy, and inflorescence structure (Goldblatt, 1990a, Goldblatt et al., 1991). Iridoideae are defined largely by a fugacious perianth and hollow, terminally stigmatic styles that divide below the anthers. These two morphological synapomorphies are supported by the presence of an unusual chemical character, free meta-carboxy amino acids (Goldblatt, 1990a), not present elsewhere in the family. In three of the four tribes of Iridoideae the style branches are further specialized in being thickened or compressed, and the apices are elaborated into crests or similar structures (Goldblatt, 1990a; Rudall, 1994).

Of the four tribes (Table 2), Sisyrinchieae are basal, while the remaining Irideae, Mariceae, and Tigridieae may be a monophyletic lineage defined by several morphological and chemical synapomorphies (Goldblatt, 1990a). Chromosomes of many Sisyrinchieae, including *Libertia* and *Orthrosanthus*, are small, generally 1–2 μm long (Figs. 7–9), and comparable in size to those of Nivenioideae. In *Sisyrinchium*, the largest genus of the tribe, the chromosomes are usually somewhat larger (Kenton & Heywood, 1984), sometimes substantially so in *Olsynium* (Kenton et al., 1987, reported as *Phaiophleps* and *Sisyrinchium* sections *Eriphilema* and *Nuno*). *Bobartia*, usually regarded as the only African genus of Sisyrinchieae, has been transferred to Irideae as a result of molecular data (Souza-Chies et al., 1997). Its comparatively large chromosomes and $x = 10$ match the plesiomorphic features of the latter tribe.

Basic chromosome number in *Libertia* is evidently $x = 19$, established for four Australasian species (Hair et al., 1967), but the only South American species counted has $2n =$ ca. 72 (Kenton & Heywood, 1984), making this possibly tetraploid if it, too, is based on $x = 19$. Base number for *Libertia* in South America still needs to be verified. In the only other American and Australasian genus of Iridaceae, *Orthrosanthus*, base number is uncertain. We have established $2n = 84$ in the Australian *O. polystachyus* (Fig. 7), also reported as $2n = 40$ (Kenton & Heywood, 1984). In the South American *O. chimboracensis* and *O. acorifolius* (Figs. 8–9) we found $2n = 54$. This accords with an earlier count of $n = 27$ for *O. chimboracensis*, based on a different collection (Goldblatt, 1982a). Kenton and Heywood (1984), however, have reported $2n = 50$ in both *O. chimboracensis* and *O. exsertus* (as var. *exsertus*). The difference in the counts seems to concern the identity of four small chromatin bodies, regarded as satellites by Kenton and Heywood, but

Table 1. New chromosome numbers in Iridaceae (Figs. 1–46) with collection data. Unless stated to the contrary, vouchers are at the Missouri Botanical Garden (MO)—herbarium acronyms are abbreviated according to Holmgren et al. (1981) and are indicated in parentheses after the collection number. Species are arranged alphabetically within the subfamilies and tribes recognized by Goldblatt (1990a).

Species	Diploid number 2*n*	Collection data
Subfamily Nivenioideae		
Aristea abyssinica Pax	64	Zimbabwe, Nyanga, *Goldblatt 9070*
A. anceps Eckl. ex Klatt	32	S. Africa, E. Cape, near Fish R. mouth, *Goldblatt 9053*
A. angolensis Baker	32	Malawi, Zomba Mt., *Goldblatt 4528*
A. juncifolia Baker	32	S. Africa, W. Cape, Cape Point Reserve, *Goldblatt 9056*
A. angustifolia Baker	32	Madagascar, Andringitra, *Goldblatt 8971*
Patersonia sericea R. Br. ex Ker Gawl.	22	Australia, NSW, Clarence, *Hind 693* (NSW)
Subfamily Iridoideae		
Tribe Irideae		
Barnardiella spiralis (N.E. Br.) Goldblatt	20	S. Africa, N. Cape, Richtersveld, *Viviers s.n.*
Dietes robinsoniana (F. Muell.) Klatt	60	Lord Howe Island, *Pickard 3377* (NSW)
Ferraria glutinosa (Baker) Rendle	40	Namibia, near Rehoboth, *Goldblatt & Manning 8808*
Iris tridentata Pursh	40	U.S.A., Florida, Leon Co., *Henderson 92-135*
Homeria hantamensis Goldblatt & J. C. Manning	12	S. Africa, N. Cape, Hantamsberg, *Goldblatt & Manning 10355*
Moraea anomala G. J. Lewis	20	S. Africa, W. Cape, Elim, *Goldblatt 361* (BOL)
M. bella Harms	12	Tanzania, Ufipa, *Goldblatt et al. 8289*
M. bipartita L. Bolus	12	S. Africa, W. Cape, *Goldblatt 4948*
M. callista Goldblatt	12	Tanzania, Kitulo Plateau, *Lovett & Congdon 2905*; Lusitu Ridge, Njombe, *Spurrier s.n.* (no voucher)
M. carsonii Baker	12	Zambia, Copperbelt, *Goldblatt 7544*
M. deserticola Goldblatt	12	S. Africa, N. Cape, Knersvlakte, *Goldblatt 9128*
M. elsiae Goldblatt	20	S. Africa, W. Cape, Kenilworth, *Esterhuysen 32358* (BOL)
M. fergusoniae L. Bolus	12	S. Africa, W. Cape, Caledon district, *Snijman 820* (NGB); Mierkraal, Bredasdorp, *Goldblatt 6186*; E. of Heidelberg, *Goldblatt 4956*; Bontebok Park road, *Goldblatt 4316A*
M. fugax (D. Delaroche) Ker Gawl.	10	S. Africa, N. Cape, Wallekraal, *Goldblatt s.n.* (no voucher)
M. incurva G. J. Lewis	12	S. Africa, W. Cape, near Tulbagh, *Hansford 1* (NBG)
M. namibensis Goldblatt	20	Namibia, Süd Witputs, *Lavranos 21257*
M. neglecta G. J. Lewis	20	S. Africa, W. Cape, Klaasjagersberg, *Goldblatt 5268*
M. tulbaghensis L. Bolus	12	S. Africa, W. Cape, near Tulbagh, *Burgers 2756* (STE)
M. schimperi (Hochst.) Pic. Serm.	12	Zaire, Shaba, *Schaijes 5108*
M. unguiculata Ker Gawl.	12	S. Africa, W. Cape, *Goldblatt 5865*
Tribe *Mariceae*		
Neomarica caerulea (Ker Gawl.) Sprague	32	ex hort., origin unknown, *Goldblatt 5930*
N. cf. *northiana* (Schneev.) Sprague	18	Paraguay, Amambay, Cerro Corá, *Solomon et al. 6950*
Trimezia martinicensis (Jacq.) Herb.	80	Venezuela, Anzoátegui, Serranía de Turimiquire, *Davidse & González 19456*; Venezuela, Mérida, Páramo de Mucubaji, *Berry 3802*
Tribe Sisyrinchieae		
Orthrosanthus polystachyus Benth.	84	Australia, ex Hort. Bot. Melbourne, *Goldblatt s.n.*

Table 1. Continued.

Species	Diploid number 2*n*	Collection data
O. acorifolius (Kunth) Ravenna	54	Venezuela, Mérida, *Grifo & Hahn 361* (BH)
O. chimboracensis (Kunth) Baker	54	Venezuela, *Dorr et al. 5044* (NY)
Sisyrinchium micranthum Cav.	48	Nicaragua, *Henrich s.n.*
Tribe Tigridieae		
Alophia drummondii (Graham) R. C. Foster	28	U.S.A., Texas, Bastrop Co., *Lee sub Goldblatt s.n.*
Calydorea azurea Klatt	28	Uruguay, Treinta y Tres to Tacuarembó, *Castillo 1146 sub Goldblatt s.n.*
C. amabilis (Ravenna) Goldblatt & Henrich	14	Argentina, Entre Ríos, Concepción del Uruguay, *Goldblatt s.n.*
C. pallens Griseb.	28	Argentina, Córdoba, Cerro Colorado, *Goldblatt s.n.*
C. xiphioides (Poepp.) Espinosa	42	Chile, Coquimbo, *Hoffmann s.n.*
Cipura paludosa Aubl.	14	Brazil, Maranhao, near Imperatriz, *Plowman et al. 9305*
Cobana guatemalensis (Standl.) Ravenna	28	Honduras, *Nelson s.n.* (no voucher)
Cypella fucata Ravenna	14	Uruguay, Maldonado, Punta del Este, *Castillo s.n.*
C. herbertii subsp. *brevicristata* Ravenna	14	Uruguay, Artigas, northern suburbs, *Castillo s.n.* (no voucher)
subsp. *wolfheugelii* (Hauman) Ravenna	14	Argentina, Buenos Aires, Cerro Ventana, *Lamberto & Möchel s.n.* (BB 3881)
C. hauthalii subsp. *opalina* Ravenna	14	Argentina, Misiones, Garruchos, *Castillo s.n.* (FAA)
Ennealophus euryandrus (Griseb.) Ravenna	14	Bolivia, Tarija, Arce, *Solomon 9972*
E. foliosus (Kunth) Ravenna	14	Peru, *Dillon 4514* (F)
Herbertia lahue Molina	42	Chile, *Ornduff 9153* (UC); U.S.A., Louisiana, Shreveport, *Heikamp, s.n.*
H. aff. *lahue*	14	Brazil, Rio Grande do Sul, Rosario do Sul, *Castillo s.n.*
H. pulchella Sweet	42	Uruguay, Maldonado, Punta del Este, *Castillo sub Goldblatt s.n.*
H. quareimana Ravenna	28	Brazil, Rio Grande do Sul, Uruguaiana, *Goldblatt s.n.*
Subfamily Ixioideae		
Tribe Watsonieae		
Micranthus junceus (Baker) N.E. Br.	20	S. Africa, W. Cape, Cape Point Reserve, *Goldblatt s.n.* (no voucher)
Thereianthus spicatus var. *linearifolius* G. J. Lewis	20	S. Africa, W. Cape, Cape Point, *Goldblatt 5400*
Watsonia dubia Eckl. ex Klatt	18	S. Africa, W. Cape, Malmesbury, *Goldblatt 8708*
W. hysterantha Mathews & L. Bolus	18 + 1B	S. Africa, W. Cape, Langebaan, *Snijman 71* (BG)
W. minima Goldblatt	18	S. Africa, W. Cape, near Greyton, *Goldblatt 8047*
Tribe Ixieae		
Crocus longiflorus Raf.	28	Italy, Sicily, Eloro, *Goldblatt 5073*
Dierama inyangense Hilliard	20	Zimbabwe, Nyanga, *Clarke s.n.* (no voucher)
Geissorhiza callista Goldblatt	26	S. Africa, W. Cape, near Grayton, *Goldblatt 8680*
G. foliosa Baker	26	S. Africa, W. Cape, Strawberry Hill, *Goldblatt 7948*
G. roseoalba (G. J. Lewis) Goldblatt	26	S. Africa, E. Cape, Pootjeshoogte, *Vlok 1663*
Gladiolus aquamontanus Goldblatt & Vlok	30	S. Africa, W. Cape, Rust-en-Vrede, *Vlok s.n.*

Table 1. Continued.

Species	Diploid number 2*n*	Collection data
G. inandensis Baker	30	S. Africa, Kwazulu-Natal, Inchanga, *Goldblatt & Manning 10057*
G. longicollis Baker	30	S. Africa, E. Cape, Naudes Nek, *Goldblatt & Manning 9542*; Mpumalanga, Long Tom Pass, *Goldblatt & Manning 9823*
G. ochroleucus Baker	30	S. Africa, E. Cape, East London, *Batten 1123*
G. oppositiflorus Hook.f.	30	S. Africa, E. Cape, near Kei Road, *Batten s.n.*
G. permeabilis subsp. *edulis* (Ker Gawl.) Oberm.	28	S. Africa, E. Cape, Rhodes, *Batten 1118*
G. phoenix Goldblatt & J. C. Manning	30	S. Africa, W. Cape, Bain's Kloof, *Goldblatt & Manning 9423*
G. pole-evansii Verdoorn	30	S. Africa, Mpumalanga, Denilton, *Goldblatt & Manning 9808*
G. pretoriensis O. Kuntze	30	S. Africa, Gauteng, Pretoria, *Goldblatt & Manning 9799*
G. saundersii Hook. f.	30	S. Africa, E. Cape, Naudes Nek, *Batten 1114*
G. stefaniae Oberm.	30	S. Africa, W. Cape, Montagu, *Manning s.n.* (NBG)
G. sulcatus Goldblatt	90	Tanzania, Njombe, Lusitu Ridge, *Spurrier 804*
G. wilsonii (Baker) Goldblatt & J. C. Manning	30	S. Africa, E. Cape, Nahoon, *Batten s.n.*
G. woodii Baker	30	S. Africa, Mpumalanga, Belfast, *Goldbaltt & Manning 9811*
Hesperantha baurii Baker	24	Swaziland, near Mbabane, *Goldblatt 6609*
H. luticola Goldblatt	26 + 1B	S. Africa, N. Cape, Hantamsberg, *Goldblatt s.n.* (no voucher)
H. radiata (Jacq.) Ker Gawl.	26	Lesotho, Blue Mountain Pass, *Schmitz 8531* (ROML)
Ixia brevituba G. J. Lewis	20	S. Africa, W. Cape, Roggeveld, *Goldblatt & Manning 8645*
I. latifolia var. *ramulosa* G. J. Lewis	20	S. Africa, N. Cape, Namaqualand, *Goldblatt 9241*
I. paniculata D. Delaroche	20	S. Africa, W. Cape, Piekenierskloof, *Goldblatt 5117*
Melasphaerula graminea (L.) N.E. Br.	20	S. Africa, W. Cape, near Soutpan, *Goldblatt s.n.* (no voucher); near Clanwilliam, *Goldblatt 3832*
Radinosiphon leptostachya (Baker) N.E. Br.	30	Malawi, Golomoti Mts., *Boussard s.n.*; Mt. Malosa, *Goldblatt 9201*
Romulea cameroonensis Baker (= *R. campanuloides* Baker)	26	Malawi, Zomba Plateau, *Goldblatt 9094*; *Snijman s.n.*
R. congoensis Bég.	ca.78	Rwanda, Virunga Mts., *D'Arcy 7887*
R. c.f. linaresii Parl.	ca.39	Greece, Athens, *Goldblatt 5051*
Sparaxis caryophyllacea Goldblatt	20	S. Africa, W. Cape, Nardouw Pass, *Goldblatt 6162*
S. parviflora (G. J. Lewis) Goldblatt	40	S. Africa, W. Cape, without precise locality (no voucher)
S. variegata subsp. *meteler-kampiae* (L. Bolus) Goldblatt	20	S. Africa, W. Cape, Algeria, *Goldblatt s.n.*
Syringodea bifucata de Vos	12	S. Africa, Gauteng, farm Sandfontein, *Davidson 3108*
Tritonia chrysantha Fourc.	22	S. Africa, E. Cape, Alicedale, *Bayliss 8047*
T. florentiae (Phill.) Goldblatt	20	S. Africa, W. Cape, Ceres Karoo, *Goldblatt 3912*
T. laxifolia Benth.	20	Tanzania, Makambako, *Spurrier 601*
T. squalida (Aiton) Ker Gawl.	22	S. Africa, W. Cape, S. of Riversdale, *Goldblatt 5090*
Xenoscapa fistulosa (Klatt) Goldblatt & J. C. Manning	22	S. Africa, N. Cape, Richtersveld, *Williamson & Hamer 4428*
X. uliginosa Goldblatt & J. C. Manning	22	S. Africa, N. Cape, Namaqualand, *Goldblatt 9244*

which we consider to be chromosomes. Ancestral base number for the genus is probably $x = 9$, not $x = 10$ as suggested by Kenton and Heywood, making the species counted in South America hexaploid. This does not explain the counts of both $2n = 40$ (by Kenton & Heywood) and 84 (by us) in the same Australian species. This species also differs from the South American species of the genus

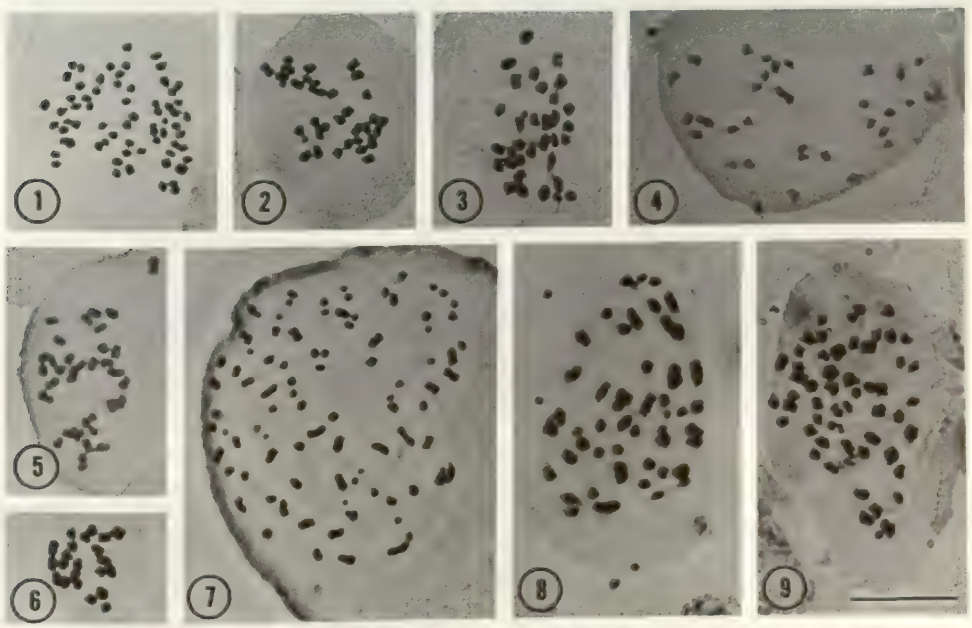
Table 2. Chromosome numbers in genera of Nivenioideae and Iridoideae. Data are largely from Goldblatt (1971, 1982a) who included reviews of previous reports for the subfamilies, and Kenton & Heywood (1984). Sources other than Goldblatt (1971) are referenced below. Numbers in parentheses after the genera indicate number of species counted out of the total in the genus; parenthetical entries in the base-number column indicate secondary base numbers. Presence of triploids, unless known to be stabilized, and B chromosomes are not included. Genera are arranged alphabetically in subfamilies and tribes according to Goldblatt (1990a) excepting that *Bobartia* has been moved from Iridoideae: Sisyrinchieae to Irideae in light of molecular data (Souza-Chies et al., 1997; M. Chase, pers. comm.).

Genus	Basic and diploid numbers		Reference
	x	2*n*	
Nivenioideae			
Aristea (12/52)	16	32, 64	Goldblatt, 1995
Geosiris (0/1)	uncounted		
Klattia (1/3)	16	32	
Nivenia (4/10)	16	32	
Patersonia (6/20)	?11	22, 42, ca.62	Goldblatt, 1979a
Witsenia (1/1)	16	32	
Iridoideae			
Tribe Sisyrinchieae			
Diplarrhena (2/2)	16	32	Kenton & Heywood, 1984
Libertia (5/8)	19	38, 76, 112	Hair et al., 1967; Kenton & Heywood, 1984
Olsynium (5/11) (incl. *Phaiophleps*)	10(9, 8, ?11)	20, 22, 40, 60, 18, 96	(as *Phaiophleps* and *Sisyrinchium* sects. *Nuno* and *Eriphilema*, e.g. Rudall et al., 1986; Rodriguez, 1986
Orthrosanthus (4/8)	?9(?12, 10)	54, 40, 84, 50	Kenton & Heywood, 1984
Sisyrinchium (40/ ca. 80)	9(8, 5, 17)	18, 36, 72, 16, 32, 48, 64, 96, 34	Rudall et al., 1986; Kenton et al., 1987
Solenomelus (1/2)	?8	48	Rudall et al., 1986
Tapeinia (0/1)	uncounted		
Tribe Mariceae			
Neomarica (4/12)	?9(8)	18, 16, 32	Goldblatt, 1982a; Kenton & Heywood 1984
Pseudotrimezia (0/6)	uncounted		
Trimezia (5/20)	?14(13, 10 or 20)	28, 26, 52, 40, 60, 80	Goldblatt, 1982a; Kenton & Heywood 1984
Tribe Tigridieae			
Ainea (0/1)	uncounted		
Alophia (3/5)	14	28	Goldblatt, 1982a; Kenton & Heywood 1984
Calydorea (4/10) (incl. *Catila*)	7	14, 28, 42	Goldblatt, 1982a; Kenton & Heywood 1984
Cardenanthus (0/8)	uncounted		
Cipura (4/8)	7	14, 28[1]	Goldblatt & Henrich, 1987
Cobana (1/1)	14	28	Ravenna, 1974
Cypella (5/20)	7(5)	14, 28, 10	
Eleutherine (2/2)	6	12[1]	Goldblatt & Snow, 1991
Ennealophus (3/5) (incl. *Tucma*)	7	14	Kenton & Heywood, 1984; Martínez & De Azkue, 1987
Fosteria (1/1)	14	28	Molseed, 1970
Gelasine (2/5)	7(6)	14, 12	Kenton & Rudall, 1987
Herbertia (4/8) (=*Trifurcia*)	7	14, 28, 42	Winge, 1959; Kenton & Heywood, 1984
Kelissa (0/1)	uncounted		
Mastigostyla (3/16)	14	28	Huynh, 1965; Martínez & De Azkue, 1987

Table 2. Continued.

Genus	Basic and diploid numbers		Reference
	x	2*n*	
Nemastylis (3/5)	7	14, 28, 56	Goldblatt, 1982a
Onira (0/1)	uncounted		
Sessilanthera (2/4)	14	28	Cruden, 1972
Tigridia (14/35)	7	14, 28	Molseed, 1970; Kenton & Heywood 1984
Tribe Irideae			
Barnardiella (1/1)	10	20	Goldblatt, 1977
Belamcanda (1/1)	16	32, 64	Nakajima, 1936; Hsu, 1971
Bobartia (8/14)	10	20	Strid, 1972
Dietes (6/6)	10	20, 40, 60	Goldblatt, 1981a
Ferraria (10/10)	10	20, 40, 60	de Vos, 1979
Galaxia (14/15)	9(8, 7, 6)	18, 16, 14, 12	Goldblatt, 1979c, 1984a
Gynandriris (7/9)	6	12, 24	Goldblatt, 1980b
Hermodactylis (1/1)	10	20	Simonet, 1932
Hexaglottis (6/6)	6(7, 5)	12, 14, 10	Goldblatt, 1987
Homeria (34/34)	6(5, 4)	12, 24, 10, 9, 8	Goldblatt, 1980a, 1981b
Iris (185/ca. 225)	? (many diploid numbers occur in this large genus; both polyploidy and dysploidy are frequent)		
Moraea (95/130)	10(9, 8, 7, 6, 5)	20, 40, 18, 16, 12, 24, 48, 10	Goldblatt, 1976, 1986a, 1986b
Pardanthopsis (1/1)	16	32	Simonet, 1932
Roggeveldia (2/2)	6	12, 24	Goldblatt, 1992

[1]Goldblatt & Snow (1991) have shown that the plants associated with the counts of $2n = 12(-14)$ for *Cipura paludosa* and $2n = 14$ for *Eleutherine bulbosa* (Sharma & Talukdar, 1959) were confused with one another. Counts of $2n = 14$ are for *C. paludosa*, while those of $2n = 12(-14)$ are for *E. bulbosa*. The count of $2n = 14$ for the latter reported by Rao (1969) is probably also for *C. paludosa*.



Figures 1–9. Mitotic metaphase in Iridaceae subfamily Nivenioideae (*Aristea* and *Patersonia*) and Iridoideae tribe Sisyrinchieae (*Orthrosanthus*).—1. *Aristea abyssinica* ($2n = 64$).—2. *A. anceps* ($2n = 32$).—3. *A. angolensis* ($2n = 32$).—4. *A. juncifolia* ($2n = 32$).—5. *A. angustifolia* ($2n = 32$).—6. *Patersonia sericea* ($2n = 22$).—7. *Orthrosanthus polystachyus* ($2n = 84$).—8. *O. acorifolius* ($2n = 54$).—9. *O. chimboracensis* ($2n = 54$). Vouchers as given in Table 1. Scale bar, 10 μm.

in having a bimodal karyotype with the larger chromosomes 2–2.3 μm long, and the smaller 0.5–1.2 μm long, a pattern also noted by Kenton and Heywood. More counts are needed in *Orthrosanthus*, for both Australian and South American taxa. Chromosomal characters will likely be relevant to the systematic and phylogenetic understanding of the genus.

We include only one original count in *Sisyrinchium* (Table 1), $2n = 48$, for the annual *S. micranthum*. This agrees with past reports for the species. Ancestral base number for *Sisyrinchium* is most likely $x = 9$. Subgenus *Echthronema* has species based on either $x = 9$, 8, or 17, but most species of subgenus *Sisyrinchium* have $x = 8$ (Kenton & Heywood, 1984) and one annual species has $n = 5$. The related *Olsynium* (including *Sisyrinchium* subg. *Eriphilema*) has base numbers of $x = 10$, 9, 8, and perhaps 11, but the ancestral base number may well be $x = 10$. We conclude that the ancestral base number for Sisyrinchieae may be $x = 10$, based on the pattern so far reported in the tribe (Table 2). The Australian *Diplarrhena*, currently included in Sisyrinchieae, has large chromosomes and $x = 16$. On the basis of chromosome size it accords better with Irideae. Number alone provides no information about its relationships.

Large chromosomes and a base number of $x = 10$ have been postulated to be ancestral for Irideae (Goldblatt, 1990a), and *Bobartia* (usually included in Sisyrinchieae), *Dietes*, and *Ferraria* (Table 2) conform to this pattern. The count here of $2n = 60$ in *D. robinsoniana* (Table 1), the Lord Howe Island endemic and only non-African species of *Dietes*, conflicts with an earlier count of $2n = 20$ in the species (Goldblatt, 1979a). It seems unlikely that *D. robinsoniana* is heteroploid. We question the identity of the plant counted earlier under that name, unfortunately without a voucher. The closely related *D. bicolor* from South Africa is also polyploid, $2n = 40$ (Goldblatt, 1971). The four other species of *Dietes* are diploid, $2n = 20$ (Goldblatt, 1981a).

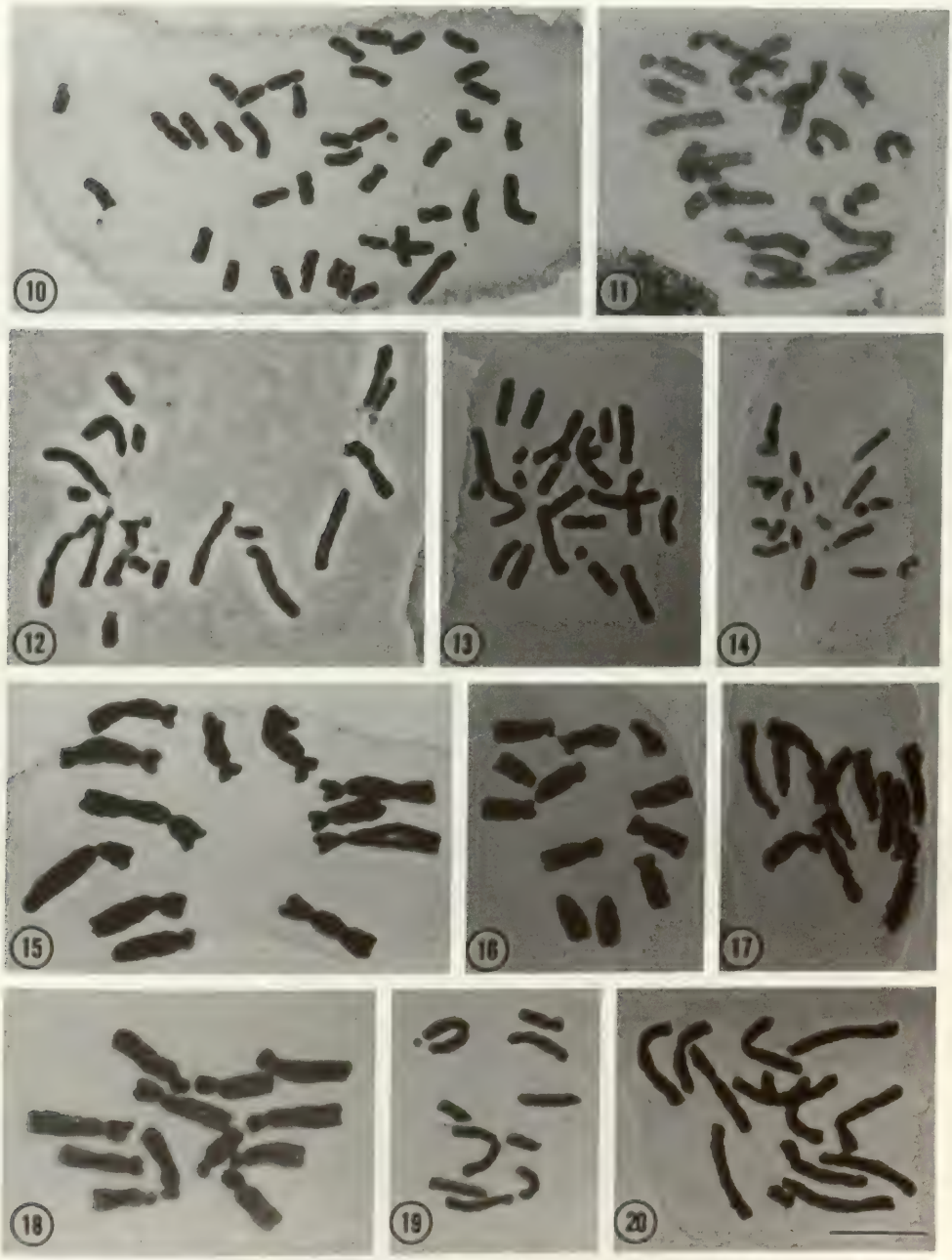
Our count here of $2n = 40$ for the tropical African *Ferraria glutinosa* confirms a report that the species is tetraploid in Namibia (Goldblatt, 1979b). Interestingly, a diploid population of the species has been reported from Zaire (De Vos, 1979), thus establishing that the species is heteroploid. Of the remaining nine species of *Ferraria*, seven are diploid, *F. divaricata* has diploid and tetraploid subspecies, and two more have both tetraploid and hexaploid populations. *Ferraria* is one of the few African genera of Iridaceae in which polyploidy appears to have played a significant role in its evolution.

Ancestral base number in the large African genus, *Moraea*, is also $x = 10$ (Goldblatt, 1976, 1986a). Our counts for numerous species of the genus with this base number show some degree of variation in their karyotypes (Figs. 11–13). Notably in subgenus *Visciramosa*, *M. elsiae* has a distinctive karyotype in which 5 of the 10 chromosome pairs are telocentric (Fig. 13). The other four species of subgenus *Visciramosa* also have this unusual and presumably derived karyotype (Goldblatt, 1971 and unpublished).

Dysploid reduction in at least four lineages of *Moraea* has resulted in the independent evolution of the secondary base of $x = 6$ (Goldblatt, 1986a). Counts reported here from subgenus *Vieusseuxia*, section *Polyanthes*, and subgenus *Grandiflora* provide examples of the three main groups with $x = 6$ (Figs. 15–18, 21–24). In a fourth lineage, *M. fugax* (subg. *Moraea*) offers a remarkable example of dysploid reduction from $x = 10$ (presumably the ancestral base) to $n = 8$, 7, 6, and 5 within a single polymorphic species (Goldblatt, 1986b). The count here of $2n = 10$ (Fig. 19) is representative of one of several cytotypes in the species.

In subgenus *Vieusseuxia*, karyotypes typically have marked size variation (Figs. 21, 22, 24), the shortest chromosome pair, 7–8 μm long, being about two-thirds to about half as long as the longest pair, 12–14 μm. One of the two longest pairs is always more or less metacentric and the other is acrocentric. A small satellite is consistently present on one of these long pairs. Chromosomes of subgenus *Grandiflora* are consistently larger than elsewhere in the genus and 10–14 μm long. In *Moraea schimperi*, typical of the subgenus (Fig. 23), the chromosomes are acrocentric to nearly telocentric and a small satellite is located on one of the nearly telocentric chromosome pairs. Based on measurement of total chromosome length, we estimate that genome size in *M. schimperi* is some 20–30% larger than in subgenus *Vieusseuxia* or subgenus *Moraea*.

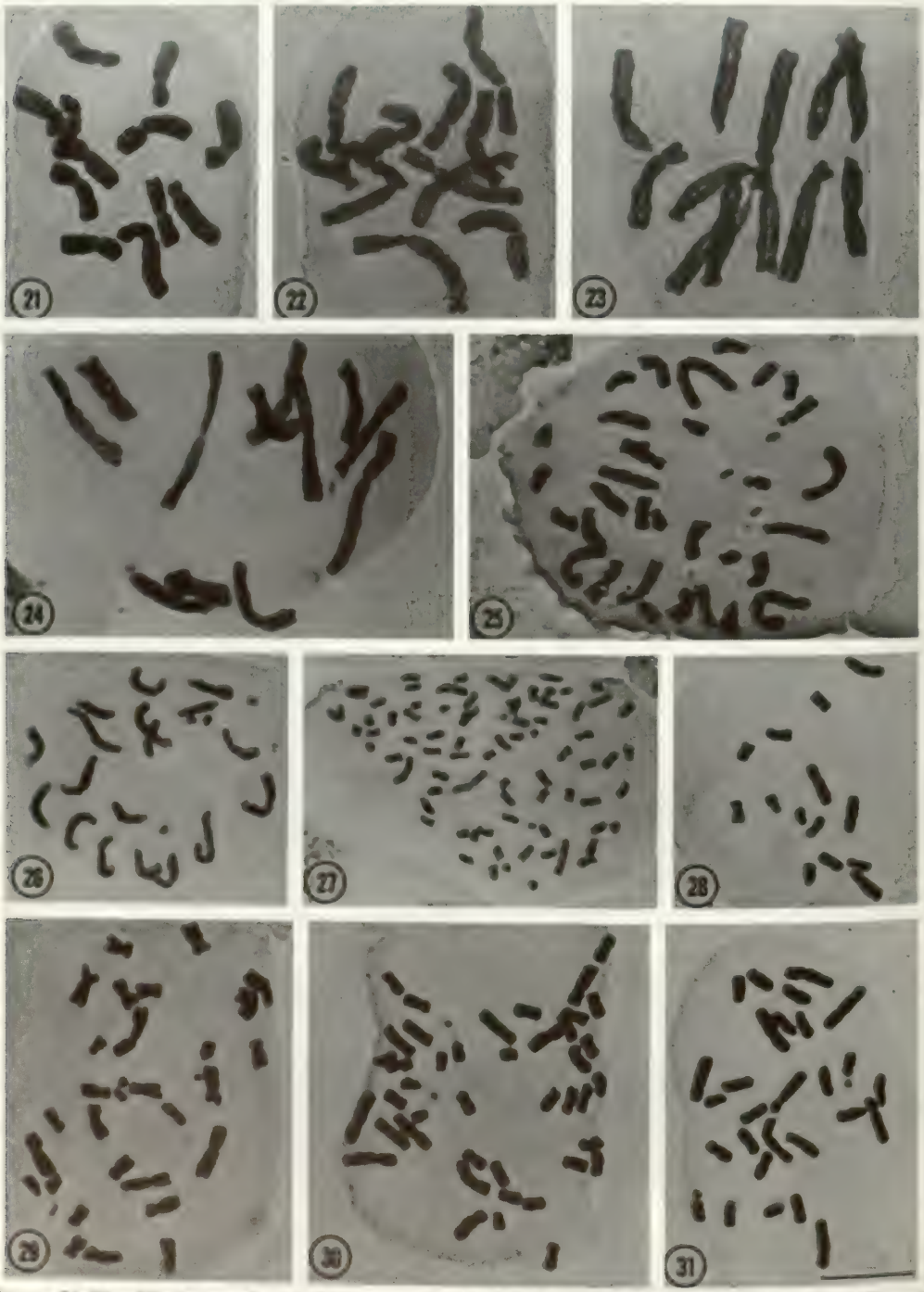
In section *Polyanthes*, e.g., *M. bipartita*, *M. callista*, *M. carsonii*, *M. deserticola* (Figs. 15–18), chromosome size variation is modest. The chromosomes are 7–12 μm long and all are more or less acrocentric. This pattern resembles closely that of the karyotypes of the southern African genera, *Hexaglottis*, *Homeria*, and *Roggeveldia* (Goldblatt, 1980a, 1987). The karyotypic similarity among these three taxa suggests common ancestry with *Moraea* sect. *Polyanthes*. This possibility should be considered in future studies of the phylogeny of Irideae. We have noted an unusual condition in *M.*



Figures 10–20. Mitotic metaphase in Iridaceae subfamily Iridoideae tribe Irideae.—10. *Iris tridentata* ($2n = 40$).—11. *Moraea anomala* ($2n = 20$).—12. *M. namibensis* ($2n = 20$).—13. *M. elsiae* ($2n = 20$).—14. *Barnardiella spiralis* ($2n = 20$).—15. *Moraea carsonii* ($2n = 12$).—16. *M. deserticola* ($2n = 12$).—17. *M. bipartita* ($2n = 12$).—18. *M. callista* ($2n = 12$).—19. *M. fugax* ($2n = 10$).—20. *M. fergusoniae* ($2n = 12$). Vouchers as given in Table 1. Scale bar, 10 μm.

callista. One population examined has a karyotype consisting of matching pairs (Fig. 46A), but another is karyotypically heterozygous (Fig. 46B) and has one long metacentric chromosome and one very short metacentric. Further studies in this tropical African species are needed to elucidate the significance of this situation.

Unusual in Iridaceae, the only three species of *Homeria* that exhibit dysploidy, *H. pallida*, $n = 6$ and 4, and *H. tenuis* and *H. flavescens*, $2n = 10$,



Figures 21–31. Mitotic metaphase in Iridaceae subfamily Iridoideae tribes Irideae (*Moraea*), Marieae (*Neomarica* and *Trimezia*), and Tigridieae (*Cypella*, *Calydorea*, and *Herbertia*).—21. *Moraea incurva* (2*n* = 12).—22. *M. tulbaghensa* (2*n* = 12).—23. *M. schimperi* (2*n* = 12).—24. *M. unguiculata* (2*n* = 12).—25. *Neomarica caerulea* (2*n* = 32).—26. *N. cf. northiana* (2*n* = 18).—27. *Trimezia martinicensis* (2*n* = 80).—28. *Cypella herbertii* subsp. *wolfheugelii* (2*n* = 14).—29. *Calydorea pallens* (2*n* = 28).—30. *Herbertia lahue* (2*n* = 42).—31. *H. pulchella* (2*n* = 28). Vouchers as given in Table 1. Scale bar, 10 μm.

9, and 8, are complex heterozygotes (Goldblatt, 1980c). The complex heterozygosity in these species is associated with dysploidy, itself evidently achieved by unequal reciprocal translocation. In *Hexaglottis*, the specialized *H. virgata* has populations with $n = 6$, 5, or 7, the latter number evidently consistent for subspecies *karooica*. In the latter there is an additional pair of very small chromosomes that resemble B chromosomes except that their number is stable. In populations of subspecies *virgata* with $n = 5$, the karyotype has an extra pair of metacentric chromosomes and the numerical change is presumed to have been accomplished by conventional Robertsonian fusion (Jones, 1974, 1977; Goldblatt, 1987).

Our counts for four populations of *Moraea fergusoniae* are $2n = 12$. The previous count of $2n = 20$ for the species (Goldblatt, 1971) is clearly incorrect. The karyotype (Fig. 20) is notable in having the two longest chromosomes acrocentric, ca. 14 μm long, and bearing very large satellites that exceed the short arms of the chromosomes. The unusual karyotype does not help assess the affinities of the species, the subgeneric disposition of which is uncertain. In its small, long-lasting flower with trilobed inner tepals it corresponds with subgenus *Vieusseuxia*, but the presence of several leaves in the species is inconsistent with that subgenus, all species of which have a single foliage leaf.

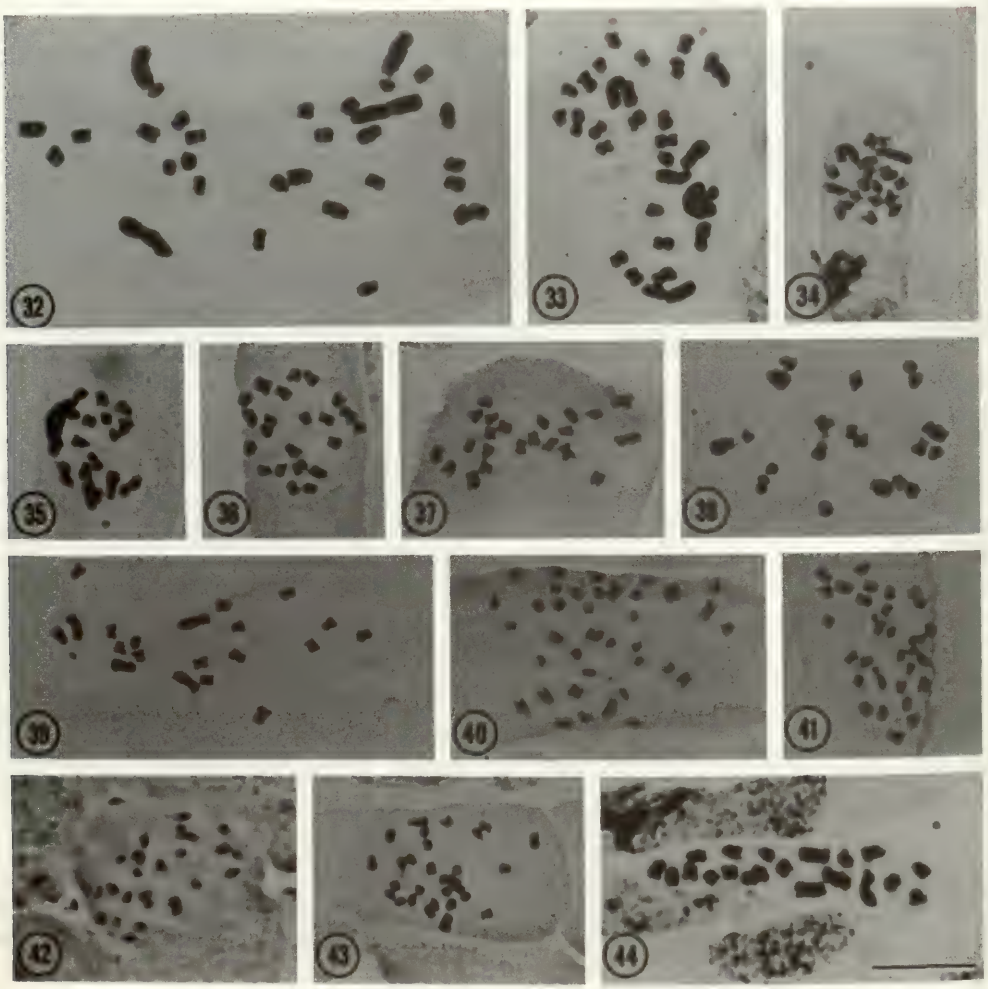
The southern African and Mediterranean *Gynandriris* also has $x = 6$ (Goldblatt, 1980b). Two species of the genus have a karyotype that accords fairly well with *Moraea* sect. *Polyanthes*, but most species have a second karyotype in which the longest pair is metacentric, a pattern reminiscent of *Moraea* subg. *Vieusseuxia*. The monotypic *Barnardiella* has $x = 10$ and a karyotype like that in many species of *Moraea* subg. *Moraea* (e.g., Figs. 11–13), also $x = 10$. In *Barnardiella* the longest chromosomes are ca. 5.6 μm and shortest ca. 2 μm (Fig. 14). Presence of blue flowers and an included ovary in *Barnardiella* point to a relationship close to species such as *M. tortilis* and *M. rigidifolia*, which have these same morphological features.

Galaxia appears to be a dysploid genus with an ancestral base of $x = 9$. The basic karyotype (Goldblatt, 1979c) broadly resembles that of the ancestral karyotype in *Moraea* except for the difference in base number and generally somewhat smaller chromosomes. The six species of subgenus *Eurystigma* display a dysploid series with different species having $x = 9$, 8, 7, and 6. This has been interpreted as a descending dysploid sequence based on the morphology of the species concerned (Goldblatt, 1979c, 1984a).

The Northern Hemisphere *Iris*, one of the two largest genera of Iridaceae, is cytologically complex, and ancestral base number is uncertain. The base number $x = 20$ is frequent in the less specialized subgenus *Limniris*, but subgenus *Iris* almost certainly has $x = 12$ (excluding polyploidy, the most common numbers are $n = 12$, 11, 10, and 9). Based on an analysis of the many counts available in the literature, subgenus *Reticulata* (sometimes treated as a genus, *Iridodictyum*) has $x = 10$ ($n = 10$, 9, 8); subgenus *Xiphium* may have $x = 18$ ($n = 18$, 17, 16, 14); and subgenus *Scorpiris* (syn. *Juno*) appears to have $x = 12$ ($n = 12$, 11, 10, 9, and even 13 and 15).

The single count included here for *Iris* was made because *I. tridentata* (subg. *Limniris*), the only North American species uncounted, was available to us. The count of $2n = 40$ and large chromosomes 3.3–6.3 μm long (Fig. 10) are consistent with several species of section *Limniris*, common numbers for which are $2n = 44$ and 40. However, our count differs from the available reports for both *I. setosa* ($2n = 38$, 36, and 54) and *I. hookeri* ($2n = 38$), the only other species of series *Tripetalae* and presumably the closest relatives of *I. tridentata* (Mathew, 1981). In their comparatively large size, the chromosomes of *Iris* species agree well with other genera of Irideae.

Basic chromosome number in Marcoeae (syn. Trimezieae), one of two exclusively New World tribes of Iridoideae (Goldblatt, 1990a), is uncertain (Table 2). Of the three genera currently recognized, *Pseudotrimezia* is uncounted and the pattern in the remaining two is confused. The five species of *Trimezia* counted (Fig. 27) have diploid numbers of $2n = 26$, 28, 40, 52, 54, 60, and 80 (Table 2), numbers that seem to have little relationship to one another. There is also a remarkable variation in chromosome size among the species counted (Kenton & Heywood, 1984). The two species with numbers based on 10, *T. martinicensis* ($2n = 40$, 80) and *T. sincorana* ($2n = 60$), also have the smallest chromosomes. They are closely related and appear to be derived on the basis of their specialized floral morphology ($2n = 54$ reported by Kenton & Heywood (1984) for *T. martinicensis*, is almost certainly based on another species). *Trimezia martinicensis* is known to be autogamous, also a derived condition. Hence, the base of $x = 10$ is probably also derived in these species. The less specialized *T. steyermarkii* has $n = 26$ and *T. martii* has $n = 14$, and the vegetatively specialized *T. fosteriana* has $n = 13$. More counts are needed in *Trimezia* before it will be possible to make sense of the pattern here. Tentatively, we suggest that $x = 14$ may be the ances-

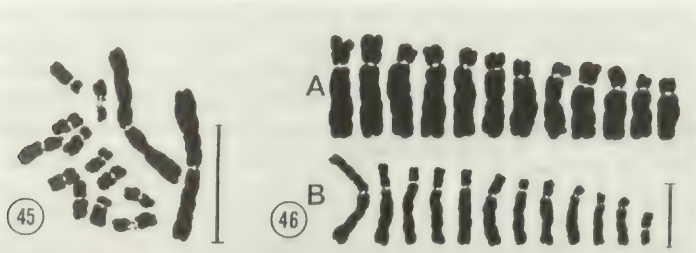


Figures 32–44. Mitotic metaphase in Iridaceae subfamily Iridoideae tribe Tigridieae and subfamily Ixioideae.—32. *Alophia drummondii* (2*n* = 28).—33. *Cobana guatemalensis* (2*n* = 28).—34. *Micranthus juncifolius* (2*n* = 20).—35. *Lapeirousia barklyi* (2*n* = 16).—36. *Xenoscapa fistulosa* (2*n* = 22).—37. *X. uliginosa* (2*n* = 20).—38. *Dierama inyangensis* (2*n* = 20).—39. *Ixia latifolia* (2*n* = 20).—40. *Sparaxis parvifolia* (2*n* = 40).—41. *Radinosiphon leptostachya* (2*n* = 30).—42. *Romulea cameroonensis* (2*n* = 26).—43. *Gladiolus ochroleucus* (2*n* = 30).—44. *Tritonia laxifolia* (2*n* = 20). Vouchers as given in Table 1. Scale bar, 10 μm.

tral base for the genus. Cycles of polyploidy and dysploid reduction then would best explain the remaining base numbers.

The related *Neomarica*, included in *Trimezia* by Ravenna (1976), is specialized in having a winged aerial stem and branches crowded apically. *Neomarica northiana* has 2*n* = 18 (Fig. 26), a count confirmed here, as does *N.* cf. *vittata* (Kenton & Heywood, 1984). Reports for *N. gracilis* include 2*n* = 18, 40, and 32. Some of these counts are almost certainly from misidentified plants. The Central American *N. variegata* (often confused with *N. gracilis* in the literature), specialized in its red, fleshy seeds, has 2*n* = 16 and *N. caerulea* has 2*n* = 32 (Fig. 25). The ancestral base number for the genus is most likely $x = 9$, and $x = 8$ is evidently derived by dysploid reduction. The variation already evident in both *Trimezia* and *Neomarica* makes it essential that chromosome cytology be included in future systematic and phylogenetic studies of these genera.

Unlike Mariceae, the pattern in the other exclusively American tribe Tigridieae is reasonably clear (Figs. 28–31). The ancestral base number appears to be $x = 7$, and this is the only base number in most genera of subtribe Cipurinae counted, and the only base in the other subtribe, Tigridiinae (Table 2). The base of $x = 7$ is strongly conserved despite a fair degree of karyotypic diversity. Bimodality is common and is also conserved despite variation in



—Figure 45. Mitotic metaphase in *Ennealophus foliosus* ($2n = 14$) (Iridoideae–Tigridieae).—Figure 46. Metaphase chromosomes of *Moraea callista* ($2n = 12$) (Iridoideae–Irideae). A: population from Lusitu Ridge with normal chromosome complement; B: population from the Kitulo Plateau showing structural heterozygosity. Vouchers as given in Table 1. Scale bar, 5 μm.

chromosome and karyotype size (Kenton et al., 1990). Among seven species of *Cypella* and *Hesperoxiphion* (a genus sometimes included in *Cypella*), all with $x = 7$, chromosome size varies considerably. A more than three-fold difference in total DNA among the species has been demonstrated by Kenton et al. (1990). Yet bimodality and relative sizes of the chromosomes within the karyotypes of each species are maintained.

A particularly distinctive karyotype is present in *Ennealophus* (including *Tucma*) (Fig. 45). All three species counted (of a total of five) have one long metacentric pair, ca. 7 μm long, and six much shorter pairs, ca. 1.5 μm long, one of which has a satellite larger than the short chromosome to which it is attached (see also Kenton & Heywood, 1984).

Cypella plumbea, sometimes segregated as *Phalocallis* (Ravenna, 1977), has $2n = 10$ and is exceptional here (counts for the few other species that have been placed in *Phalocallis* would be interesting). The two species of *Eleutherine*, an apparently very derived genus, have $x = 6$ (Goldblatt & Snow, 1991) as does *Gelasine intermedia* (= *G. azurea*). The latter is an autogamous, complex heterozygote (Kenton & Rudall, 1987) with an apparently derived floral morphology. The only other species of *Gelasine* counted has $2n = 14$ (Ravenna, 1984).

Polyploidy is common in Tigridineae, and a few genera are exclusively polyploid. In *Tigridia* most species so far counted (e.g., Figs. 32, 33) have $x = 14$ (Table 2), including all those from Central America and Mexico (Molseed, 1970; Kenton & Heywood, 1984), but at least two South American species have $n = 7$. The only counts in *Alophia* (the species of which are sometimes confused nomenclaturally with those of *Herbertia*), *Fosteria*, *Cobana*, and *Sessilanthera* are $2n = 28$. At least the three latter, all small genera closely related to Central American *Tigridia*, and probably nested within it, may be exclusively tetraploid. Despite their polyploidy, karyotypes in *Cobana*, *Alophia*, *Tigridia*, and their allies consistently have one long metacentric chromosome pair and one submetacentric pair. In *Cobana* (Fig. 33) it is possible to tell by careful observation that the long and apparently submetacentric chromosome pair is actually acrocentric with a long satellite attached to the short chromosome arm. The mismatch of the four long chromosomes suggests early chromosomal rearrangement in a polyploid ancestor of the group or a hybrid origin from parents with different karyotypes.

3. IXIOIDEAE

Small chromosomes, usually 1–2.5 μm long (Figs. 34–44), are plesiomorphic in this, the largest subfamily, and are found in most genera (Goldblatt, 1971). Ixioideae are otherwise defined by several morphological and palynological features (Goldblatt, 1990a; Goldblatt et al., 1991). By fusion one or more larger chromosome pairs have evolved in some genera, notably *Lapeirousia* (Goldblatt & Takei, 1993) and *Crocus* (Brighton, 1976; Brighton et al., 1983). In *Lapeirousia* the two long chromosomes present in all species are 4.1–6.5 μm long, and in most species the remaining 12–18 chromosomes are 1–2 μm long, thus typical of Ixioideae. Basic numbers are generally high in the subfamily (Table 3). Dysploidy and the development of secondary base numbers, known in a few genera, are discussed below.

Freesia, including the species of *Anomatheca* transferred here (Goldblatt & Manning, 1995), and *Xenoscapa* (Figs. 36, 37) have $x = 11$ and all species counted are diploid, $2n = 22$ (Table 3). Similar karyotypes with $x = 11$ characterize most species of *Tritonia* and *Crocosmia*, genera that are closely allied to one another and probably closely related to *Freesia* (Goldblatt, 1971,

Table 3. Chromosome numbers in genera of Ixioideae. Data largely from Goldblatt (1971), who included references to earlier studies. Other sources are referenced below. Numbers in parentheses after the genera indicate number of species counted out of the total in the genus; parenthetical numbers in the base number column indicate secondary base numbers. Presence of triploids, unless known to be stabilized, and B chromosomes are not included in the table.

Genus	Basic and diploid numbers		Reference
	x	2*n*	
Tribe Pillansieae			
Pillansia (1/1)	10	40	Goldblatt & Takei, 1993
Tribe Watsonieae			
Lapeirousia (32/40)	10(9, 8, 6, 5, 4, 3)	20, 18, 16, 12, 10, 8, 6	Goldblatt, 1990b; Goldblatt & Takei, 1993
Micranthus (3/3)	10	20	
Savannosiphon (1/1)	8	16	Goldblatt & Marais, 1979
Thereianthus (3/7)	10	20	
Watsonia (31/52)	9	18	Goldblatt, 1989a
Tribe Ixieae			
Babiana (20/64) (incl. *Antholyza*)	7	14	
Chasmanthe (2/3)	10	20	
Crocosmia (6/9)	11	22	de Vos, 1984
Crocus (79/ca.80)	?6 (uncertain: many base numbers recorded including much polyploidy, sometimes within a species, Mathew, 1982)		
Devia (1/1)	10	20	Goldblatt & Manning, 1990
Dierama (7/44)	10	20	
Duthieastrum (1/1)	10	20	de Vos, 1974b (as *Duthiella*)
Freesia (13/15) (incl. *Anomatheca*)	11	22	Goldblatt, 1972 (as *Anomatheca*), 1982b
Geissorhiza (43/82)	13	26, 39, 52	Goldblatt, 1985
Gladiolus (85/255) (incl. *Homoglossum*)	15(14, 13, 12, 11)	30, 60, 90, 120, 28, 26, 24, 22	Goldblatt et al., 1993
Hesperantha (32/ca. 65) (incl. *Schizostylis*)	13(12)	26, ca.50, ca.72–76	Goldblatt 1984b
Ixia (14/45)	10	20, 40	
Melasphaerula (1/1)	10	20	(not $x = 11$, Goldblatt, 1971)
Radinosiphon (1/1)	15	30	
Romulea (ca.80/ca. 90)	13 or 12(14, 11, 10, 9)	26, 28, 24, 22, 20, 18, 30, 52, 78	de Vos, 1972
Sparaxis (10/13) (incl. *Synnotia*)	10	20, 40	
Syringodea (7/8)	6(11)	12, 22	de Vos, 1974a
Tritonia (15/28)	11(10)	22, 20, 44	de Vos, 1982
Tritoniopsis (6/22) (incl. *Anapalina*)	?16(15)	32, 30	Goldblatt, 1990c
Xenoscapa (2/2)	11	22	Goldblatt, 1972 (*as Anomatheca*)
Zygotritonia (1/4)	7	14	Goldblatt, 1989b

1991; Shneyer, 1990; Rudall & Goldblatt, 1991). Counts here for *T. florentiae* and *T. laxifolia* (Fig. 44), $2n = 20$, are the first records for both species and the only counts in the genus not based on $x = 11$. We assume that these are examples of dysploid reduction by fusion. *Tritonia florentiae* is specialized in *Tritonia* in being acaulescent, or almost so, and it does not seem closely related to *T. laxifolia*, indicating independent dysploid reduction twice in the genus. *Chasmanthe* and *Devia*, evidently closely related to *Tritonia* and *Crocosmia* (de Vos, 1984; Goldblatt & Manning, 1990), have $x = 10$, additional examples of dysploid reduction in this alliance. *Du-*

thieastrum, which may be another specialized derivative of this group, also has $x = 10$.

Counts here for *Dierama*, *Ixia*, and *Sparaxis*, all $x = 10$, are consistent with several other reports for these genera (Goldblatt, 1971). There is, however, an important difference between their karyotypes. In *Dierama* and *Ixia* the karyotypes are bimodal, with two relatively long pairs 2.3–2.6 μm long, and eight shorter pairs 1–1.7 μm long (Figs. 38–39), but in *Sparaxis* (Fig. 44) the chromosomes are all small, 0.9–1.6 μm long (Fig. 40). In two of the species of *Ixia* in which we could distinguish satellites, *I. polystachya* and *I. latifolia*, they were attached to the long arms of long chromosomes (Fig. 39). How consistent this is in *Ixia* is uncertain, but in *I. acaulis* (Goldblatt & Manning, 1993) the satellites (not illustrated there) are in the normal position on the distal end of the short arms of two long chromosomes. In *Dierama* and *Sparaxis* the satellites are in the conventional position on the short arm of a long chromosome pair. Earlier reports of the satellites on short chromosome arms in *Ixia* (Goldblatt, 1971) should be confirmed using more refined techniques.

The difference between the karyotypes of *Sparaxis* (now including *Synnotia*) and *Dierama* and *Ixia*, the two genera with which it has often been closely associated (Lewis, 1954, Goldblatt, 1969), suggests that the affinities of *Sparaxis* may lie elsewhere, or at least are not close to the aforementioned genera. Fundamental differences in their leaf margin anatomy (Rudall & Goldblatt, 1991) support this contention. The count here for *S. parviflora* (Goldblatt, 1991) is the first record of polyploidy in the genus (but this should be confirmed for additional populations).

Our counts for two populations of the monotypic African genus, *Radinosiphon*, $2n = 30$ (Fig. 41), confirm past reports for this genus (Table 3), apparently related to *Gladiolus*, which has the same ancestral base number and similar karyotype (Goldblatt et al., 1993). Total chromosome length in *Radinosiphon* is some 10–15% less than in several species of *Gladiolus* that we have examined, but the significance of this in connection with their possible close relationship cannot yet be assessed. Counts here for *Gladiolus*, $2n = 30$ for 12 species, $2n = 28$ for *G. permeabilis* subsp. *edulis*, and $2n = 90$ for the tropical African *G. sulcatus*, include the first reports for nine species. The karyotypes are consistent with the majority of counts for the genus. The count of $2n = 28$ for *G. permeabilis* does not accord with previous counts for the species. Most likely the population we examined is dysploid and not representative of the entire species or even subspecies.

In the monotypic, western southern African *Melasphaerula* we found $2n = 20$ in two separate populations (Table 1). We suspect that the only other count for the genus, $2n = 22$ (Goldblatt, 1971), is incorrect. *Melasphaerula* is believed to be most closely related to *Geissorhiza* and *Hesperantha*, with which it shares woody corm tunics. The two latter genera have an ancestral base number of $x = 13$ (Goldblatt, 1971, 1984b), a marked difference from the base number in *Melasphaerula*. Additional counts here (Table 3) for *Geissorhiza* and *Hesperantha* confirm $x = 13$ and the predominance of diploidy, $2n = 26$, in both genera. Our count for the eastern southern African *H. baurii*, $2n = 24$, establishes a new, and evidently, secondary base number in *Hesperantha*. More counts for this widespread and common southern African species and its close relatives are needed before the significance of our report of dysploidy can be gauged.

Our observations here for *Romulea cameroonensis* (Fig. 42) and *R. congoensis* are consistent with the small chromosome size (ca. 0.9–2.2 μm) and range of base numbers reported for the genus (de Vos, 1972). However, our count of $2n = 26$ in *R. cameroonensis* (Fig. 42), based on plants from tropical Africa, differs from de Vos's report of $2n = 22$ for the species (as *R. campanuloides*) in southern Africa. The possibility that tropical and southern African plants assigned here are different species should be considered. *Romulea congoensis*, $2n =$ ca. 78 and not before counted, appears to be hexaploid on a base of $x = 13$. The population of *R. linaresii* from Greece with $2n =$ ca. 39 studied here may be triploid (on a base of $x = 13$) or alternatively tetraploid on a base of $x = 10$. Particularly small chromosomes in the species make accurate counting difficult.

The ancestral base number for *Romulea* was suggested by de Vos (1972) to be $x = 12$, but $x = 13$, which seems to be an equally likely ancestral base, is common. Lower base numbers in *Romulea*, $x =$ 11, 10, and 9, seem almost certainly to be derived and occur in specialized lineages. The question of ancestral base number in the genus should be reexamined in the light of phylogeny, at present poorly understood. If *Romulea* is related to *Geissorhiza* and *Hesperantha* as suggested by Goldblatt (1991) then an ancestral base number of $x = 13$ seems likely for the genus on the basis of outgroup comparison.

The single count reported here for *Crocus* (Table 1), $2n = 28$ in *C. longiflorus*, confirms past records for that species, as does the count for *Syringodea*

bifucata (= *S. bicolor*), $2n = 12$. The latter count is for plants from Gauteng Province, South Africa, where the genus was not recorded until 1983 (de Vos, 1983). Basic number in *Syringodea* is most likely $x = 6$.

The ancestral base number for Ixioideae is most likely $x = 10$, evidently the base number for tribes Pillansieae and Watsonieae (Table 3). The ancestral base number in Ixieae may also be $x = 10$, but genera less specialized as regards leaf anatomy and seed characters (Goldblatt & Manning, 1995) have higher base numbers, and it is equally likely that $x = 10$, present in a few genera of the tribe, is secondary. At least *Geissorhiza*, *Gladiolus*, *Hesperantha*, *Radinosiphon*, *Romulea*, and *Tritoniopsis*, all with ancestral base numbers between $x = 16$ and 13 (Table 3), are paleopolyploid. We suspect that *Syringodea* ($x = 6$) is a dysploid derivative of an ancestor shared with *Romulea*. Both have inflorescences reduced to solitary flowers and similar asymmetric corms with woody tunics. The single species of *Syringodea* with $x = 11$ (Goldblatt, 1971; de Vos, 1976) is almost certainly a secondary hypotetraploid. Notably low base numbers characterize *Babiana* and *Zygotritonia* (Table 3); although both have $x = 7$, they are probably not closely related (Goldblatt, 1989b).

Extensive dysploid series in Ixioideae are restricted to just 4 genera, *Lapeirousia*, *Gladiolus*, *Romulea*, and *Crocus*, out of a total of 28. Limited intrageneric dysploidy occurs in *Syringodea*, as noted above, and is reported here for the first time in two species of *Tritonia* and one of *Hesperantha*. Thus, the pattern outlined by Goldblatt (1971) for Ixioideae of genera each having a single base number must be modified. Although most genera do have a single base number and exhibit little or no polyploidy, significant dysploidy has been discovered in *Gladiolus* since that review (Goldblatt et al., 1993). Most species of the genus have $x = 15$, but among the small-flowered tropical African species numbers include $n = 14$, 13, 12, and 11. The pattern of dysploidy in *Lapeirousia* has also been found to be more extensive than previously thought (Goldblatt, 1990b). As hypothesized by Goldblatt and Takei (1993) there is a striking example of dysploid reduction from $x = 10$ to 4 followed by polyploid increase and further reduction from $n = 6$ to $x = 3$ in *Lapeirousia* subg. *Paniculata*. *Gladiolus* and *Lapeirousia* must, therefore, be added to the list of genera of Ixioideae that have extensive dysploid sequences.

Dysploid trends appear consistently to be descending sequences. In *Tritonia flavescens* and *Syringodea unifolia* the species are evidently derived in their respective genera, the first specialized in its acaulescent habit and the second in having a solitary and terete leaf. In *Gladiolus* all the dysploid species appear more specialized than those with the presumably ancestral $x = 15$ (Goldblatt et al., 1993). Moreover, they appear to belong to at least three, and probably four, separate lineages. Likewise, in *Romulea* members of primitive sections have $x = 12$ or 13, and those of derived sections have $x = 11$, 10, or 9 (de Vos, 1972).

Cytological patterns in *Crocus*, last of the genera of Ixioideae with extensive dysploidy, are complex (Mathew, 1982) and remain to be satisfactorily explained. Both dysploidy and polyploidy have been significant in the cytological evolution of the genus. Provisionally we suggest an ancestral base of $x = 6$ for the genus, a hypothesis based on outgroup comparison (the immediately related *Syringodea* has $x = 6$) and on the pattern of counts in section *Crocus* (summarized by Mathew, 1982), which includes the more primitive members of the genus. From this base we assume dysploid reduction to $x = 4$, perhaps in several lines, and repeated polyploidization on bases of 6, 5, 4, and 3.

REVIEW OF GENOME SIZE

Genome sizes have been established for a number of Iridaceae and, as in many other families, have been found to vary considerably, even within genera. In Iridoideae, species of *Sisyrinchium* (Kenton et al., 1987) have basic genome sizes (adjusted for polyploidy), i.e., 1C values, of 0.48–0.73 pg in subgenus *Sisyrinchium* (= sect. *Bermudiana*) and 0.25–2.10 pg in subgenus *Echthronema*. The related *Olsynium* (= *Phaiophleps* plus *Sisyrinchium* sections *Filifolium* and *Nuno*) typically has larger genomes among the temperate southern South American species with 2.66–3.26 pg, but the octoploid North American member of the genus, *O. douglasii*, has a basic genome size of 0.49 pg.

Among Tigridieae, which typically have larger chromosomes than *Sisyrinchium*, 1C genome sizes range from 2.03–2.39 pg in *Cypella* and 1.24–1.34 pg in three species of *Hesperoxiphion* (Kenton et al., 1990), but *H. huilense* has a genome size of 4.38 pg, despite also being diploid. These genome sizes were determined cytophotometrically against a standard, *Hordeum vulgare*, genome size of which is 11.12 pg (2C) or 5.56 pg (1C), a value recently confirmed by Arumuganathan and Earle (1991). Comparable genome sizes of 1.47–2.48 have also been reported by Martínez and De Azkue (1987) for five species of *Eleutherine*, *Ennealophus*, and

Mastigostyla, but *Calydorea* sp. has a smaller genome of 0.98 pg.

Among Old World Iridoideae, Irideae have comparatively larger genomes than Tigridieae, although genome sizes vary considerably among diploid members of the tribe (Goldblatt et al., 1984). Genome sizes reported by Goldblatt et al. (1984) using *Zea mays* as a standard need correcting. Genome size in maize has now been found to be C = 4.75–5.63 pg (Arumuganathan & Earle, 1991; Bennett & Smith, 1991), somewhat lower than the estimate of 6.3 pg used by Goldblatt et al. The 4C values published by Goldblatt et al. (1984) thus require adjustment by a factor of 0.75–0.84. We make a correction of 0.75 here in the figures given below (the strain used in the Goldblatt et al. study had a karyotype without knobs or structural additions). Basic 1C genome sizes (corrected for polyploidy) in Irideae are 1.20 pg in *Galaxia* to 12.24 pg in *Iris histrio*.

Moraea, the only genus investigated extensively, has larger basic genomes in subgenus *Vieusseuxia*, 4.93–6.81 pg ($x = 6$) than in subgenus *Moraea*, 3.74–4.32 ($x = 10$). In *Homeria* (including *Sessilistigma*) and *Hexaglottis* (both $x = 6$) 1C genomes range from 3.87 to 5.94 pg in the five species examined. The larger genomes evident in *Moraea* subg. *Grandiflora* (discussed above) have not yet been measured for total DNA. One species of *Iris*, *I. histrio* ($2n = 20$), has a 1C genome size of 12.24 pg. *Iris* itself, or at least subgenus *Reticulata* to which *I. histrio* belongs, may be paleopolyploid. The specialized, acaulescent *Galaxia* has the smallest reported genome in Irideae, 1.2 pg, about one-third the size of that in its closest allies (*Moraea* subg. *Moraea*), a puzzling observation.

Genomes are smaller in Ixioideae (Olszewska & Osiecka, 1982; Goldblatt et al., 1984; Goldblatt & Takei, 1993). Using the above correction factor when necessary, 1C genome sizes range from 1.01 pg (or 0.54 pg for the basic genome) in the paleotetraploid *Pillansia* to 0.60 pg in *Gladiolus* (even lower estimates for *Hesperantha* and *Anomatheca* obtained by Goldblatt et al. (1984) are probably not reliable). In *Lapeirousa* genomes ranging from 1.27 to 1.45 pg (corrected for intrageneric polyploidy) were established by Masterson (in Goldblatt & Takei, 1993) using *Nicotiana tabacum* L. as a standard. *Lapeirousia* is evidently unusual in Ixioideae in having genomes as large as those in *Galaxia* (Irideae) and some Tigridieae. Genome sizes reported by Olszewska and Osiecka (1982) in general confirm the above pattern, but as chromosome numbers were not provided for the plants that they studied, corrections for polyploidy are not possible. Their estimate of a 1C value of 1.1 pg for *Crocosmia* ×*crocosmiiflora* (as *Tritonia*) is, however, consistent with the pattern for Ixioideae. Their reports for *Crocus vernus* (Ixioideae) of 11.56 pg and 2.1 pg for *Iris sibirica* (Iridoideae) may be reversed. *Iris sibirica*, normally $2n = 28$, has much larger chromosomes than *Crocus vernus*, in which diploid numbers of $2n = 8$, 10, 12, 16, 18, and 20 are known (Brighton, 1976).

Genome size sometimes reflects taxonomic relationship, but it is clearly influenced by environmental factors as well, and gross differences between taxa may have little taxonomic significance above species rank. On the other hand, there seems to be a correlation between genome size and species relationships in *Moraea*. In subgenus *Vieusseuxia* ($x = 6$) species have consistently larger genomes than do species of subgenus *Moraea* or the related genus *Dietes* (both $x = 10$). Still larger genomes characterize subgenus *Moraea* and subgenus *Grandiflora* ($x = 6$).

MODES OF NUMERICAL CHANGE

Most generic ancestral base numbers in Iridaceae are relatively high (Tables 2, 3), which suggests an early burst of polyploidy in the evolution of the family or a paleopolyploid origin for the family. Low ancestral base numbers for Tigridieae ($x = 7$), and for *Babiana* and *Zygotritonia* ($x = 7$) and *Syringodea* ($x = 6$) (all Ixioideae), appear to represent paleodiploidy, but we suspect that these base numbers are most likely derived. The latter would be more consistent with their levels of morphological specialization. Neopolyploidy (defined here as intrageneric polyploidy) is common in Northern Hemisphere representatives of the family and is estimated here to be above 60%. For example, in *Gladiolus* 5 polyploid species, 1 of them with diploid races, are known in the 80 species counted from sub-Saharan Africa and Madagascar, but all the 6 to 10 species of the genus that occur in Eurasia and North Africa are tetraploid ($4x$) to dodecaploid ($12x$). Neopolyploidy in African members of the three subfamilies of Iridaceae occurring in sub-Saharan Africa is remarkably low on a world scale. Some 5% of the species of Ixioideae and 10% of Iridoideae are polyploid, and 10% more species of the latter have both diploid and polyploid populations. No species of African Nivenioideae are exclusively polyploid, but 3 species of 24 counted (12%) have diploid and tetraploid races.

Polyploidy appears to be more important in the evolution of South and Central American Iridaceae. Nearly all Central and North American Tigridieae

are tetraploid or hexaploid, including the 10 species of *Tigridia* counted, 2 of 3 species of *Nemastylis* counted, and all 3 species of *Alophia* in the region. One population of a Mexican species of *Tigridia* has a diploid race, and at least two South American species of this genus are diploid. The genera *Fosteria* and *Cobana*, closely allied to *Tigridia*, are apparently exclusively polyploid. In other genera that are moderately well known cytologically, like *Herbertia* and *Cipura*, more than half of the species counted are polyploid. Polyploidy seems equally important in other tribes of Iridoideae in South America, but except for *Sisyrinchium*, the genera are too poorly known cytologically for useful comparisons to be made. For *Sisyrinchium*, subgenus *Sisyrinchium* seems to have over 90% of the species polyploid, while subgenus *Echthronema* has about 75% of the species tetraploid.

Dysploidy (stepwise change in base number) is important in several genera of Iridaceae, and extensive dysploid sequences are described in more detail above for *Crocus*, *Gladiolus*, *Lapeirousia*, and *Romulea* (Ixioideae) and *Galaxia* subg. *Eurystigma* and *Moraea* (Iridoideae). Outgroup comparison and/or correlated morphological specializations in dysploid species consititute compelling evidence that decreasing dysploidy has been the dominant or exclusive factor in numerical change in these genera. Less extensive dysploid changes in *Gelasine*, *Hesperantha*, *Homeria*, and *Tritonia* should also be regarded as having proceeded from higher to lower base number for the same reasons. In the one species of *Hexaglottis* mentioned above there are examples of both descending and apparent ascending dysploidy. Thus in Iridaceae, all but one of the numerous examples where the direction of dysploid change can be determined, the direction is downward. This is consistent with Jones's (1977) hypothesis that most cases of dysploid change in plant families are downward. Ascending dysploidy is probably a rare phenomenon in natural populations, and arguing from the information about dysploidy in Iridaceae and a few other families, we question whether it has played a significant role in the evolution of any plant group.

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CHROMOSOMAL OBSERVATIONS ON THE ALZATEACEAE (MYRTALES)[1]

Frank Almeda[2]

Abstract

Alzatea verticillata Ruiz & Pav. subsp. *amplifolia* S. A. Graham of the monotypic neotropical family Alzateaceae has a haploid chromosome number of $n = 14$. This first report for the family is unique as a putative base number among the 14 core families of the Myrtales. Given that $x = 12$ appears to be the basic number for the order, $n = 14$ could have arisen as an ascending dysploid or as a tetraploid derived from an ancestral base number of $x = 7$. A summary of probable basic chromosome numbers is given for all families currently recognized in the Myrtales except the Crypteroniaceae, which remains unknown cytologically.

Alzatea is a monotypic genus of shrubs or small trees restricted to low montane cloud forest habitats from Costa Rica and Panama south to Andean South America from Colombia to Bolivia. The placement of this genus in eight families in five orders since its discovery nearly 200 years ago (Graham, 1984) has stimulated considerable research in the last two decades aimed at assessing its relationships and taxonomic status. Several recent papers have brought to light data from macromorphology, anatomy, chemistry, embryology, palynology, DNA sequencing, and cladistic analysis that support the recognition of *Alzatea* as a distinct family within the angiosperm order Myrtales (Dahlgren & Thorne, 1984; Graham, 1984; Graham & Averett, 1984; Johnson & Briggs, 1984; Keating, 1984; Patel et al., 1984; Tobe & Raven, 1984; van Vliet & Baas, 1984; Conti et al., 1996; Conti et al., in press). I here add chromosome information for the Alzateaceae that fills a notable gap in the knowledge of cytology in the order.

Materials and Methods

Flower buds were collected from a natural population in the field, fixed in modified Carnoy's solution (4 chloroform, 3 ethanol, 1 glacial acetic acid, v/v/v) for 24 hours, then transferred to 70% ethanol for refrigerated storage. Anthers were teased open and the contents squashed in 1% ferric aceto-carmine. Counts were made from pollen mother cells using a Zeiss light microscope with phase contrast and a 100× oil immersion objective. Drawings of meiotic configurations were made by camera lucida at a magnification of 1500×. The voucher collection for the count reported here is as follows:

Alzatea verticillata Ruiz & Pav. subsp. *amplifolia* S. A. Graham. $n = 14$. Panama. Chiriquí: Fortuna Dam area in the vicinity of Centro de Investigaciones Jorge Arauz, 1200 m, 8 Feb. 1996, *Almeda et al. 7545* (CAS).

Observations and Discussion

The first chromosome count for this monotypic family, $n = 14$, is based on diakinesis figures and one telophase I figure (Fig. 1). Meiosis was regular in all cells examined. Chromosome clumping at metaphase I and telophase I presented some interpretation difficulties, but examination of numerous diakinesis figures provided clear and consistent counts of 14.

Chromosome numbers are now known for representative species of all core families in the Myrtales except the Crypteroniaceae. Excluding the Alzateaceae, base chromosome numbers are established with some certainty for 9 of the other 13 families in the order (Table 1). Four or possibly five of the families have $x = 12$, the number most commonly postulated as the original base number for the order (Raven, 1975; Johnson & Briggs, 1984). As noted by Graham et al. (1993), $x = 12$ is also the only base number occurring in each of the major evolutionary lineages hypothesized for the Myrtales by Johnson and Briggs (1984). The lowest base numbers in the order are $x = 8$ for the

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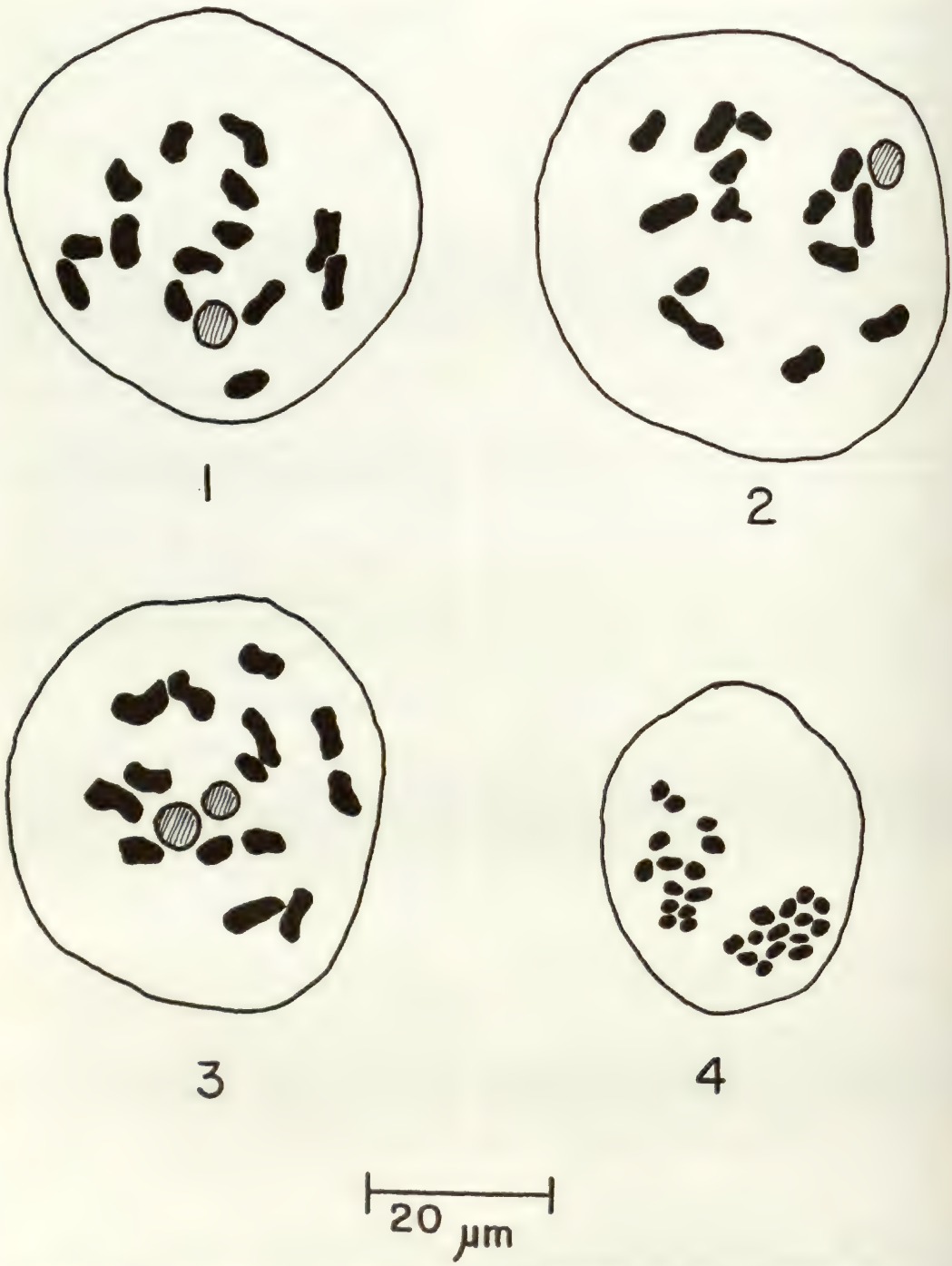
[2] Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118, U.S.A.



Figures 1–4. Camera lucida drawings of meiotic chromosome figures of *Alzatea verticillata* subsp. *amplifolia*.—1–3. Diakinesis (n = 14).—4. Telophase I (n = 14).

Table 1. Base chromosome numbers of core families in the Myrtales.

Family	Base number (x)	References
Alzateaceae	14?	This paper
Combretaceae	12	Raven, 1975
Crypteroniaceae	?	—
Heteropyxidaceae	12	Fernandes, 1971
Lythraceae	8	Graham, pers. comm. in Raven, 1975; Tobe et al., 1986
Melastomataceae	9 or 12	Almeda, unpublished
Memecylaceae	7?	Favarger, 1952, 1962; Solt & Wurdack, 1980
Myrtaceae	11	Smith-White, 1959; Rye, 1979
Oliniaceae	10?	Goldblatt, 1976
Onagraceae	11	Raven, 1975
Penaeaceae	10	Dahlgren, 1968, 1971
Psiloxylaceae	12	Johnson & Briggs, 1984
Rhynchocalycaceae	10	Goldblatt, 1976; Johnson & Briggs, 1984
Trapaceae	12	Raven, 1975

Lythraceae and possibly $x = 7$ for the Memecylaceae (Table 1), both of which were very likely derived by descending dysploidy from the ancestral base. The chromosome number reported here for the Alzateaceae would not be discordant with what is known about base numbers in the order. The process by which it evolved, however, is open to speculation.

Accepting the premise that chromosome numbers higher than $n = 13$ are considered to be of polyploid derivation (Grant, 1963, 1981), then $n = 14$ for *Alzatea* could be interpreted as a tetraploid based on $x = 7$. Recent collections from South America have extended the geographic ranges for each of the two subspecies of *Alzatea*, and, not surprisingly, diminished the perceived morphological distinctions between them (Graham, 1995). Chromosome information for the nominate subspecies of *Alzatea* is needed before $x = 7$ can be ruled out as an extant base number for the family since intraspecific polyploidy is known in species of other myrtalean families such as the Lythraceae (Graham, 1989), Melastomataceae (Almeda, in press), Onagraceae (Berry, 1982; Raven & Tai, 1979), and Myrtaceae (Rye, 1979).

Given the range of base numbers in the Myrtales, another less parsimonious scenario that could account for the origin of $n = 14$ is descent from a tetraploid ($n = 16$) based on $x = 8$. A parallel example has been postulated by Graham (1992) to account for $x = 15$ in *Diplusodon* of the Lythraceae.

An alternative scenario that could also account for the origin of $n = 14$ would be dysploid increase from the ancestral base of $x = 12$. Given that ascending dysploidy is believed to be four times less common in the flowering plants than descending dysploidy (Jones, 1970; Goldblatt & Poston, 1988), one could argue that this scenario is less likely, but it certainly is not implausible.

A base number of 7 or 14 would serve to underscore the uniqueness of Alzateaceae but would provide no additional insights about relationships that have not already been demonstrated using other lines of evidence. Information amassed to date shows that the Alzateaceae and the Rhynchocalycaceae share a common ancestor that, in turn, is closest to the Penaeaceae, Oliniaceae, and Crypteroniaceae (Graham, 1984; Johnson & Briggs, 1984). Chromosome data are lacking for the latter family. The Penaeaceae and Rhychocalycaceae both have $x = 10$ (Table 1). The Oliniaceae are in need of additional study to confirm the few known counts that are also suggestive of $x = 10$ (Goldblatt, 1976). The fact that *Alzatea* is sister to the three families with $x = 10$ or 10? in the clade Alzateaceae–Rhynchocalycaceae–Penaeaceae–Oliniaceae (Conti et al., 1996) lends further support to descending dysploidy as the likely mechanism for chromosome number changes in *Alzatea*. Chromosome information can sometimes inform us in ways that morphological data cannot. In this instance, if $x = 14$ is ultimately established as the base number for *Alzatea*, it may prove to be the only family-level lineage in the order that originated via polyploidy.

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NOTICE

PLANT EVOLUTION AND DOMESTICATION
26-27 SEPTEMBER 1997

Indiana University will hold a weekend symposium in honor of Dr. Charles Heiser's prominent contributions to Botany during his 50 years at IU. The symposium is entitled "Plant Evolution and Domestication," and will take place Friday evening, September 26 and all day Saturday, September 27. Speakers include Greg Anderson, John Doebley, Jeff Doyle, Don Levin, Barbara Pickersgill, Charles Rick, Loren Rieseberg, Doug Soltis, and Herb Wagner. Registration fees are $75.00 for regular participants and $25.00 for students. For further information contact Angi Bailey or Jennifer Jones, Department of Biology, Indiana University, Bloomington, IN 47405-6801. Phone: 812-855-6283, FAX: 812-855-6705, email: abailey@bio.indiana.edu.

Editor's Note

With this issue of the *Annals*, we witness a change in editorship. Henk van der Werff, who has successfully led the journal through the past five years, passes the editorial pen to Michael H. Grayum. Beginning in 1992 with volume 79 issue 1 and continuing with contributions to the current issue, Henk has provided leadership, sound scientific judgment, and a keen editorial eye, for which the readership of the *Annals* and those of us responsible for its production are grateful. It is with heartfelt thanks that we acknowledge Henk's significant contributions to the journal, and his continued involvement as a member of the Editorial Committee. We also welcome with great enthusiasm the new editor, and wish him well in the many challenges that lie ahead.

Editorial Staff of the *Annals of the Missouri Botanical Garden*

Editors of the *Annals of the Missouri Botanical Garden*

This information was taken from the covers of the *Annals* or from separately published volume front matter. No individual editor(s) can be identified for volumes 1–13. The title for what I call the editor varies slightly through the years, e.g., Editor of Publications, Editor, Editor-in-Chief. Through most of its history, a single individual produced the *Annals*: reviewed manuscripts, edited them, saw them through production, and got the issues distributed, although editorial asssistants were listed irregularly through the years. Beginning in the mid-1980s an assistant did much of the copy-editing. The journal is now edited by a scientific editor, responsible for technical review of manuscripts, and a managing editor, who along with with an editorial assistant, handles the manuscripts from the time they are accepted through their production and distribution in issues of the *Annals*. The *Annals* has usually been a quarterly; volumes 53–61 were complete in three numbers, and volumes 50 and 51 contained a single issue, numbered 1–4.

1914–1915: George T. Moore, Benjamin Duggar, Jacob R. Schramm, Editorial Committee, vols. 1, 2.
1916–1926: George T. Moore, Benjamin Duggar, Editorial Committee, vols. 3–13.
1919–1957: Nell C. Horner, vols. 6–44.
1958–1962: Robert L. Dressler, vols. 45–49.
1963: No editor listed, vol. 50.
1964–1968: Walter H. Lewis, vols. 51–55.
1969: Derek Burch, vol. 56(1, 2).
1969–1974: Marshall R. Crosby, vols. 56(3)–61.
1975–1981: Gerrit Davidse, vols. 62–68(1–3).
1981–1986: Nancy Morin, vols. 68(4)–73.
1987: George K. Rogers & Nancy Morin, vol. 74(1).
1987–1990: George K. Rogers, vols. 74(2)–77(2).
1990–1991: Marshall R. Crosby, vols. 77(3)–78.
1990– : Amy Scheuler, Managing Editor, vols. 77(2)– . [Amy Scheuler McPherson, 1994–.]
1992–1997: Henk van der Werff, vols. 79–84(2).
1997– : Michael H. Grayum, vols. 84(2)–.

Marshall R. Crosby
April 30, 1997

Volume 84, Number 2, pp. 167–310 of the ANNALS OF THE MISSOURI BOTANICAL GARDEN
was published on June 17, 1997.

Experimental and Molecular Approaches to Plant Biosystematics

The proceedings of the Fifth International Symposium of the International Organization of Plant Biosystematists (IOPB)

Edited by Peter C. Hoch and A. G. Stephenson

Twenty-three original contributions that span the breadth of biosystematics, a dynamic field of study that bridges the realms of systematics and population biology. The papers are arranged in four groups, reflecting the original four symposia of the 1992 meeting. *DNA and Plant Biosystematics* presents innovative work that uses the rapidly developing nucleic acid methods adapted from molecular biology. *Plant Growth Patterns and Biosystematics* includes comparative and developmental analyses of plant architecture and branching patterns. *Plant Reproductive Strategies* surveys new approaches in the analysis of plant reproductive biology, an area central to both systematic and population-level studies. *Phylogenetic Analysis and Population Biology* emphasizes the application of the powerful new methods of phylogenetic analysis to problems at the species and population levels. Monographs in Systematic Botany from the Missouri Botanical Garden, Volume 53. ISBN: 0-915279-30-4. 416 pp. Illustrated. 1995. $60.00 U.S. $62.00 Non-U.S.

Annals of the Missouri Botanical Garden, Volume 82, Number 2: Alternative Genes for Phylogenetic Reconstruction in Plants

A symposium cosponsored by the American Society of Plant Taxonomists and the Botanical Society of America, organized by Pamela S. Soltis and Douglas E. Soltis, and presented at the 1993 AIBS meetings.

Although the chloroplast gene *rbc*L has been successfully used to reconstruct plant phylogeny, many important questions of plant phylogeny and evolution cannot be addressed using it. The contributors to this issue of the *Annals* explore the potential of eight alternative genes or DNA regions for phylogenetic reconstruction at a variety of hierarchical levels. Both nuclear and chloroplast genes are evaluated. Three regions of the nuclear ribosomal RNA cistron are explored: the 18S gene, the internal transcribed spacers (ITS), and the 26S gene. Small multigene families from the nuclear genome may also carry phylogenetic signal: the phytochrome gene family and the small heat shock gene family. Three genes from the chloroplast genome are also considered: *atp*B, *ndh*F, and *mat*K. Each paper describes the location, size, structure, and rate of evolution of the chosen gene and discusses its potential for phylogenetic study. This issue also contains: "The Comparative Pollination and Floral Biology of Baobabs (*Adansonia*–Bombacaceae)" by David A. Baum and "In Memoriam: *Peter G. Martin.*" Annals 82(2) 1995. 174 pages. $27.50 U.S. $28.00 Non-U.S.

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CONTENTS

The Genus *Lycianthes* (Solanaceae) in Venezuela ..... *Carmen Benítez de Rojas & William G. D'Arcy* 167

Dialypetalanthus fuscescens Kuhlm. (Dialypetalanthaceae): The Problematic Taxonomic Position of an Amazonian Endemic ..... *Frederic Piesschaert, Elmar Robbrecht & Erik Smets* 201

Conspectus of the Genus *Palicourea* (Rubiaceae: Psychotrieae) with the Description of Some New Species from Ecuador and Colombia ..... *Charlotte M. Taylor* 224

Palynology, Phylogenetic Reconstruction, and Classification of the Afro-Madagascan Genus *Aristea* (Iridaceae) ..... *Peter Goldblatt & Annick Le Thomas* 263

Chromosome Cytology of Iridaceae—Patterns of Variation, Determination of Ancestral Base Numbers, and Modes of Karyotype Change ..... *Peter Goldblatt & Masahiro Takei* 285

Chromosomal Observations on the Alzateaceae (Myrtales) ..... *Frank Almeda* 305

Notice 309

Editor's Note and Editors of the *Annals of the Missouri Botanical Garden* 310

Cover illustration. *Eccremocarpus viridis* Ruiz & Pavón, by Phyllis Bick.

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amcpher@admin.mobot.org (editorial queries)
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A REVISION OF *PHILODENDRON* SUBGENUS *PHILODENDRON* (ARACEAE) FOR MEXICO AND CENTRAL AMERICA[1]

Thomas B. Croat[2]

MISSOURI BOTANICAL

OCT 3 1 1997

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Abstract

This is the first revision of *Philodendron* subg. *Philodendron* since that of K. Krause in *Das Pflanzenreich* in 1913. *Philodendron* subg. *Philodendron*, the largest of the three subgenera, includes 103 taxa (95 species and 8 subspecies or varieties) for Central America. Sixty-eight taxa are new to science. These include 62 species: *P. albisuccus* Croat, *P. alticola* Croat & Grayum, *P. angustilobum* Croat & Grayum, *P. annulatum* Croat & Grayum, *P. antonioanum* Croat, *P. aromaticum* Croat & Grayum, *P. bakeri* Croat & Grayum, *P. breedlovei* Croat, *P. brewsterense* Croat, *P. brunneicaule* Croat & Grayum, *P. chiriquense* Croat, *P. chirripoense* Croat & Grayum, *P. clewellii* Croat, *P. coloradense* Croat, *P. copense* Croat, *P. correae* Croat, *P. cotobrusense* Croat & Grayum, *P. cotonense* Croat & Grayum, *P. crassispathum* Croat & Grayum, *P. cretosum* Croat & Grayum, *P. dodsonii* Croat & Grayum, *P. dolichophyllum* Croat, *P. dominicalense* Croat & Grayum, *P. dwyeri* Croat, *P. edenudatum* Croat, *P. ferrugineum* Croat, *P. findens* Croat & Grayum, *P. folsomii* Croat, *P. fortunense* Croat, *P. gigas* Croat, *P. granulare* Croat, *P. grayumii* Croat, *P. hammelii* Croat, *P. hebetatum* Croat, *P. heleniae* Croat, *P. immixtum* Croat, *P. jefense* Croat, *P. knappiae* Croat, *P. lazorii* Croat, *P. lentii* Croat & Grayum, *P. llanense* Croat, *P. madronense* Croat, *P. malesevichiae* Croat, *P. morii* Croat, *P. niqueanum* Croat, *P. pirrense* Croat, *P. pseudauriculatum* Croat, *P. purulhense* Croat, *P. roseospathum* Croat, *P. scalarinerve* Croat & Grayum, *P. sousae* Croat, *P. squamicaule* Croat & Grayum, *P. squamipetiolatum* Croat, *P. straminicaule* Croat, *P. sulcicaule* Croat & Grayum, *P. thalassicum* Croat & Grayum, *P. tysonii* Croat, *P. ubigantupense* Croat, *P. utleyanum* Croat, *P. verapazense* Croat, *P. wilburii* Croat & Grayum, *P. zhuanum*; 6 infraspecific taxa: *P. davidsonii* Croat subsp. *bocatoranum* Croat, *P. hederaceum* (Jacq.) Schott var. *kirkbridei* Croat, *P. ligulatum* Schott var. *heraclioanum* Croat, *P. ligulatum* Schott var. *ovatum* Croat, *P. roseospathum* Croat var. *angustilaminatum* Croat, *P. wilburii* var. *longipedunculatum* Croat & Grayum; and 2 new combinations: *P. hederaceum* (Jacq.) Schott var. *oxycardium* (Schott) Croat, *P. radiatum* Schott var. *pseudoradiatum* (Matuda) Croat. Species diversity of *P.* subg. *Philodendron* in Central America shows a general diminution from Mexico to Middle America, followed by a marked increase closer to South America. Mexico has 21 taxa, Guatemala 15, Belize 9, El Salvador 5, Honduras 13, Nicaragua 18, Costa Rica 49, and Panama 80, respectively. Endemism is high, especially for Panama where 39 taxa are currently considered endemic. Mexico and Costa Rica each have 7 endemic species. With the exception of Belize, which has 1 endemic, no other country in Middle America has any endemic species. Only 26 species (28 taxa), a total of 26% of all Central American species, range into South America, 8 species (7% of the total) only to Colombia.

[1] This study was completed with support from National Science Foundation grant BSR-8614777.

[2] P. A. Schulze Curator of Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

Introduction

Philodendron is, after *Anthurium*, the largest genus in the Araceae, with 700 or more species (Croat, 1979, 1983a, 1988, 1990). This is the first major revision of *P.* subg. *Philodendron* for Central America since Kurt Krause's (1913) generic treatment in *Das Pflanzenreich. Philodendron* is one of the most important genera in the Neotropics, inhabiting a wide range of mesic habitats from sea level to over 2000 m and in life zones (Holdridge, 1967) ranging from *Tropical moist forest* to *Premontane rain forest.* While most species occur in virgin humid forests, the genus is known from freshwater swamps, stream banks, regrowth forest, rock outcrops, and roadbanks. It is not only one of the largest genera in the Neotropics but also often constitutes the most conspicuous element of the vegetation because of its abundance, primarily climbing habit, and frequently large, showy leaves. The genus provides a wide variety of choice ornamental plants for horticulture, including most of the species treated here. Unfortunately, it is also still poorly known taxonomically, especially in the South American Andes.

Philodendron has 119 Central American species comprising 128 taxa, distributed in two subgenera of *Philodendron.* This Central America revision encompasses only members of *P.* subg. *Philodendron,* with 103 taxa, including 95 species and 8 varieties or subspecies (Appendix 1, Geographic Distribution of Central American *Philodendron* subg. *Philodendron*). A total of 68 taxa are new to science: 62 species, 6 subspecies or varieties, and 2 combinations. Alternatively, *P.* subg. *Pteromischum,* revised separately by Grayum (1996), contains 21 species (26 taxa) for Central America. That revision encompasses all species from Pacific and Caribbean tropical America, ignoring only species from the region of the Guianas and from the Amazon drainage of South America.

Philodendron is a distinct genus, not easily confused with any other, though closest to *Homalomena,* which differs in having a consistently terrestrial habit, frequently spiny petioles, a sap smelling of anise, and staminodia among the pistillate flowers.

Species diversity of *P.* subg. *Philodendron* in Central America shows a general diminution from Mexico to Middle America with the lowest totals just north of the San Juan depression, followed by a marked increase approaching the South American continent. Mexico has 21 taxa, Guatemala 15, Belize 9, El Salvador 5, Honduras 13, Nicaragua 18, Costa Rica 48, and Panama 82. Endemism is high, especially for Panama where 39 taxa are currently considered endemic. Mexico and Costa Rica each have 7 endemic species. With the exception of Belize, which has 1 endemic, no other country in Middle America has any endemic species.

Most of the Central American species of *P.* subg. *Philodendron* (Appendix 3, Sectional Composition of *Philodendron* subg. *Philodendron* in Central America) are in *P.* sect. *Calostigma* (Schott) Engl. with 52 taxa (48 species) and *P.* sect. *Philodendron* with 62 taxa (58 species). Other sections represented in Central America are: *P.* sect. *Tritomophyllum* (Schott) Engl. with 6 species; *P.* sect. *Polytomium* (Schott) Engl. with 3 species (4 taxa); and *P.* sect. *Macrogynium* Engl. with 1 species. Sections not represented in Central America are: *Schizophyllum* (Schott) Engl.; *Camptogynium* K. Krause; and *Philopsammos* G. S. Bunting. A key for the sections of *P.* subg. *Philodendron* is included under "Taxonomy."

Materials and Methods

This revision is based on more than 25 years of field studies in Central and South America, between 1967 and 1993. All but 15 of the 95 species were studied in the field or under cultivation at the Missouri Botanical Garden. Those only known from herbarium material are: *P. breedlovei, P. brewsterense, P. chirripoense* Croat & Grayum, *P. cotobrusense, P. dwyeri, P. folsomii, P. hammelii, P. jefense, P. madronense, P. roseospathum* var. *angustilaminatum, P. sousae, P. ubigantupense, P. utleyanum,* and *P. verapazense* Croat. Except for these, all descriptions have been prepared from both living and dried specimens. The use of ("dried") preceding all or any part of the description is an indication that all that follows is based on herbarium material only. Morphological characters were coded directly into a computerized database to ensure parallel and sortable descriptions. The aroid descriptions database, completely rewritten since the publication of my revision of *Anthurium* sect. *Pachyneurium* (Croat, 1991), contains 892 character states used to describe the morphological diversity expressed in *Philodendron.* A total of 108 of these are used exclusively for description of the bisexual inflorescence (and thus were not used in the descriptions of *Philodendron*), while 220 describe unisexual inflorescences. The database also allows for sorting of characters for use in writing keys or in providing useful lists of characters for preparing a cladistic survey. In addition, the database can be put to future use for the preparation of floristic surveys or for adding additional newly discovered species. The description database is tied directly to the nomen-

clatural database in TROPICOS (Crosby, 1986; Crosby & Magill, 1986). Finally, discussions and references to illustrations as well as exsiccatae are stored separately but tied to a particular species description and to the nomenclatural information by a unique taxon number. Specimens can be added to the exsiccatae almost until the time of publication because they are automatically presorted to localities before being printed. Species descriptions are decoded into narrative text automatically before final editing for style.

Terminology and usage in the descriptions in this revision are largely defined by Croat and Bunting (1979). Further definitions of petiole cross-sectional shapes are defined and illustrated in Croat (1983a). The colors reported in the description frequently are taken from the color chart by Berlin and Kay (1969) and are referenced in the text as B & K. This color chart, available from the University of California Press, is a reproduction of the Munsell Color Array of 40 hues, at maximum saturation, with nine degrees of brightness. This represents 40 hues in the vertical columns and 9 degrees of brightness in the horizontal columns. Colors are arranged in 10 basic clusters with 4 different hues per cluster, ranging from red through yellow, green, blue, purple, and finally red-purple. The four columns for each color cluster are numbered 2.5, 5, 7.5, and 10. These numbers are repeated for each basic color type. The colors from the B & K color chart are read by first reporting the color, then the row followed by the column. For example, the third color in the fifth row is Red 5/7.5. The second color in the eighth row is Red 8/5.

Ecological zones, though sometimes estimated from my own experience with Central American vegetation, are largely taken from Holdridge life-zone maps (Holdridge, 1967; Holdridge et al., 1971), where they exist for Central American countries. Vegetation types for Mexico are taken from the "Mapa de tipos de vegetación de la República de Mexico" (Flores et al., 1971).

Each life zone is represented by a full textual statement and abbreviation which appear on life zone maps. The Holdridge Life Zones of Central America and areas where *Philodendron* occur are listed here, arranged in a generally drier to wetter order: *Tropical thorn woodland* (T-tw); *Tropical dry forest* (T-df); *Tropical moist forest* (T-mf); *Tropical wet forest* (T-wf); *Tropical rain forest* (T-rf); *Premontane thorn woodland* (P-tw); *Premontane moist forest* (P-mf); *Premontane wet forest* (P-wf); *Premontane rain forest* (P-rf); *Tropical Lower Montane wet forest*; (TLM-wf); *Tropical Lower Montane rain forest* (TLM-rf); *Tropical wet forest* transition to *Premontane wet forest* (T-wf/P-wf); *Premontane wet forest* transition to *moist forest* (P-wf/mf); and *Premontane wet forest* transition to *rain forest* (P-wf/rf).

Herbarium material has been widely distributed, and original field vouchers are cited for all herbaria whose material was seen. Herbarium material may consist of one of three kinds: (1) complete original sets (wild collected); (2) sterile original material with an inflorescence added from a cultivated plant of the same number; and (3) material collected entirely from cultivated plants. Specimens based entirely or in part on cultivated material are clearly indicated on the herbarium label.

Herbarium specimens were borrowed from most major herbaria including: AAU, B, BBS, BISH, BM, BR, CAS, CAY, CM, COL, CR, DAV, DUKE, DS, EAP, ECON, ENCB, F, FLAS, FSU, FTG, G, GH, HBG, ISC, K, L, LA, LL, LE, M, MEXU, MICH, NY, PMA, RSA, S, SCZ, SEL, TEX, U, UC, UMO, US, VEN, and WIS.

Descriptions are mostly parallel and as complete as possible. Descriptions of the pistils, vitally important in the infrageneric classification of *Philodendron*, are particularly detailed. In order to avoid repetition, description references are made to Style Types discussed by Mayo (1986). These style types are discussed and illustrated (Fig. 469) in the introduction under the section on "Morphology of Reproductive Structures—Gynoecium."

Infraspecific categories in this work adhere to the following definitions. Subspecies are those infraspecific taxa that are mostly or entirely allopatric either geographically, elevationally, or ecologically. Varieties, though morphologically distinct in one or several characters, are apparently geographically, elevationally, or ecologically sympatric. All infraspecific taxa within Central American *Philodendron* subg. *Philodendron* are ecologically sympatric.

ACKNOWLEDGMENTS

This revision could not have been completed without the help of many people, most important among them my dedicated and able co-worker, Petra Malesevich, who participated in nearly every phase of the work. I could count on her to continue the research unabated during my long field trips. Along with Bob Magill, she revised, updated, and improved the more powerful description program that we used for the *Philodendron* revision. Jo Ann Beiser played an important role for nearly two years, providing assistance in the preparation of descriptions. Kathy Pickett Upton, former Research Greenhouse manager, played a major role in maintaining the live collections, making pollinations,

and in dealing with label problems. Very special thanks also go to my colleague and fellow aroid specialist Mike Grayum, whose knowledge of the Costa Rican Araceae is without parallel. He has not only made many of the best collections of *Philodendron*, but his breadth of experience in that part of Central America and his vivid insights into the interrelationships of species were very rewarding. In addition, his skills as an editor and his knowledge of Latin and rules of nomenclature contributed much to this work. Simon Mayo, like Mike Grayum, conducted extensive work on *Philodendron*. Their work was concurrent or preceded my own, and their ideas and interpretations of phenomena in the genus were ever insightful. My own work has benefited greatly from their work. Dan Nicolson was always generous with his time in helping to solve nomenclatural problems as well as problems with translations of difficult Latin phraseology. Gordon McPherson provided pickled material of many species of *Philodendron* during his tenure as our resident botanist in Panama. Eleanor Sauer has proofread or written Latin diagnoses for nearly all of the new species. Joseph Tosi, of the Tropical Science Center in San José, Costa Rica, assisted us in standardizing our use of the Holdridge Lifezone System, which we have added to our computerized database. Leland Russell, summer volunteer and later summer employee while vacationing from his undergraduate studies at Carleton College in Minnesota, became very skillful at dissections of *Philodendron* inflorescences. His critical comparative study of the Central American species of *Philodendron* went a long way in increasing our understanding of the differences within the genus. Finally, I would like to thank my wife, Patricia, who has without complaint allowed me to spend several months each year wandering the tropics of Central and South America for almost three decades. She was always available to solve every computer glitch and has also helped with the computerized sorts of information which led to the construction of the keys.

History of the Genus *Philodendron*

Although *Philodendron* apparently figured in pre-Columbian folklore, art, and medicine during the 16th century, and herbarium material was collected by Georg Marcgraf as early as 1644 (Mayo, 1990), it was Charles Plumier who made the first effective introduction of the genus to European scientists (Mayo, 1990). He collected five or six species from Martinique, St. Thomas, and Hispaniola, giving phrase names beginning with "Arum" or "Dracunculus." See Mayo (1990) for a detailed account of *Philodendron* collections made by other late 17th-century and 18th-century explorers, including Hans Sloane in Jamaica and N. J. Jacquin in the West Indies, Colombia, and Venezuela.

Plumier's expeditions resulted in the first species of *Philodendron* to be published as new to science, albeit as an *Arum*, *A. lingulatum* L., a member of *Philodendron* subg. *Pteromischum*. His trips also resulted in *Philodendron hederaceum*, the first member of *P.* subg. *Philodendron* to be published new to science, as *Arum hederaceum* Jacq.

Heinrich Wilhelm Schott

One hundred thirty-six years passed from the time Plumier first introduced plants of what came to be known as *Philodendron* to European scientists in 1693 and the first circumscription of the genus by Schott in 1829. During this interim a number of workers, including Carl Linnaeus, worked with generic concepts and decided that not all aroids belonged in the same genus. *Arum* came to be used only for the European plants it now represents and *Arisaema*, *Dracunculus*, and *Colocasia* were also separated by the early 18th century (Hermann, 1698; Tournefort, 1700). By the fifth edition of *Genera Plantarum* Linnaeus (1754) had recognized also *Calla*, *Dracontium*, and *Pothos* as well as *Orontium*, *Pistia*, and *Acorus*, although not recognizing the last three as related to *Arum*.

By the middle of the 18th century the exploration of the Neotropics was well under way. The introduction of so many new plants from the New World tropics, including many *Philodendron* species, made it clear that further separation was needed. Because of the uncritical acceptance of many aberrant elements into *Arum* during the course of the 18th century a number of taxa now recognized as *Caladium*, *Philodendron*, and *Syngonium* were incorporated into *Arum*. Ventenant (1800) solved part of the problem by recognizing *Caladium*, but Willdenow (1805) erred in transferring into *Caladium* four of Jacquin's West Indian *Philodendron* species (all considered *Arum* at the time).

Even by the time of the 16th edition of *Systema Vegetabilum* Sprengel (1826) did not distinguish *Philodendron* but had increased the number of genera to 12, adding *Ambrosina*, *Arisarum*, *Caladium*, *Gymnostachys*, and *Zantedeschia*.

Resolution of many of the remaining generic problems with the Araceae awaited Austrian botanist Heinrich Wilhelm Schott, who was the first to focus on the taxonomy of the Araceae (Nicolson, 1960). Schott was uniquely qualified in this regard, having spent four years in Brazil collecting plants

and with access to the large collection of living plants at the Imperial Gardens [of the Hapsburg's] at Schönbrunn Palace in Vienna where he worked as the director. These included his own Brazilian collections as well as those of N. J. Jacquin from the Caribbean. In 1829 Schott described the genus *Philodendron* (published as *Philodendrum*) Schott in one of his first publications after returning from Brazil in 1821. The first species placed in the genus were: *P. grandifolium* (Jacq.) Schott, *P. laciniosum* Schott, *P. tripartitum* (Jacq.) Schott, *P. lacerum* (Jacq.) Schott, *P. pinnatifidum* (Jacq.) Schott, and *P. hederaceum* (Jacq.) Schott. In 1832 Schott published a preliminary classification of the Araceae in a work entitled *Meletemata Botanica,* which included many plant families and was done in conjunction with his colleague S. Endlicher. In this work he recognized 39 genera of Araceae including *Philodendron* and some other by now well known species-rich genera such as *Anthurium, Syngonium, Dieffenbachia, Aglaonema,* and *Spathiphyllum.* In this work he also published the first infrageneric system of classification for *Philodendron,* although it contained only three groups still recognized today. Though Schott subsequently continued to work on his circumscription of the genera and species of the Araceae for the remainder of his career, he did not publish any major revisions of Araceae for 24 years.

Endlicher (1837), publishing alone but with the obvious assistance of Schott (Mayo, 1990), produced a revision of *Philodendron* that differed from the *Meletemata Botanica* account by Schott only in having a more complete generic description, including vegetative details which were presented for the first time.

Shortly after Endlicher's revision, K. S. Kunth (1841) published in his "Enumeratio Plantarum. . ." the first species-level revision of *Philodendron.* This revision included new species and new combinations and for the first time included species of the genus that would later be recognized as members of *P.* subg. *Pteromischum.*

It was not until Schott's (1856) publication of a work entitled *Synopsis Aroidearum* that a fully developed infrageneric system of classification was realized. This was Schott's first species-level revision of the genus, and the *Synopsis* divided the genus into 22 "greges" grouped in 7 unnamed categories arranged in increasing order of complexity of leaf blade shape (Mayo, 1990). A total of 99 species (which was recognized here for the first time as grex *Pteromischum*) and 3 species of *P.* subg. *Meconostigma* were included (two of them reported as members of grex *Sphincterostigma*).

Schott's final classification of *Philodendron* was published four years later in the *Prodromus Systematis Aroidearum* (1860), a more rigorous work that came to be his last comprehensive self-published work, since he died at the age of 71 in 1865. This revision included 110 genera; almost all are still recognized as genera or subgenera. The fact that his work has stood the test of time is a testimony to the serious nature of the research he had done in Vienna during his long period of seeming inactivity.

Schott's treatment of *Philodendron* in the *Prodromus* differed from his revision in the *Synopsis* in having more complete descriptions, using more inflorescence characters; in having six rather than seven unnamed categories of leaf shape to group the "greges"; and in beginning to make use of the cataphyll (prophyll in the strictest modern sense) as a character. Schott used the term "subopposite stipule" for the feature that came to be known as the cataphyll in Engler's usage. This has proven to be one of the best and most reliable characters for the genus. For a detailed listing of the key characters for *Philodendron* used in Schott's *Prodromus* revision, refer to Mayo (1990: 50).

The *Prodromus* treatment included 135 species of *Philodendron* included in the same "greges." Twenty species of the total were members of *P.* subg. *Pteromischum* Schott and 6 species are now placed in *P.* subg. *Meconostigma* (Schott) Engl. (3 in grex *Meconostigma* and 3 in grex *Sphincterostigma*). Thus Schott included 110 names of *P.* sect. *Philodendron.* Taking synonymy into account, only 76 species of *P.* sect. *Philodendron* were included in this 1860 revision. Only 18 names pertained to Central America. Of these, only 8 are accepted members of *P.* sect. *Pteromischum.*

The species included by Schott (1860) in each grex of the *Prodromus* for Central America are listed below:

Grex *Baursia* Rchb. ex Schott: *P. wendlandii* Schott
Grex *Pteromischum* Schott: *P. aurantiifolium* Schott, *P. ligulatum* (L.) K. Koch, *P. seguine* Schott, *P. inaequilaterum* Liebm.
Grex *Canniphyllum* Schott: (no species represented)
Grex *Glossophyllum* Schott: (no species represented)
Grex *Solenosterigma* Klotzsch: *P. oxycardium* Schott, *P. micans* K. Koch, *P. scandens* K. Koch & Sello = (*P. hederaceum*)
Grex *Psoropodium* Schott: *P. tenue* K. Koch & Augustin, *P. gracile* Schott

Grex *Achyropodium* Schott: *P. verrucosum* L. Mathieu ex Schott

Grex *Platypodium* Schott: *P. pterotum* K. Koch & Augustin, *P. fragrantissimum* (Hook.) Kunth

Grex *Cardiophylacium* Schott: *P. brevispathum* Schott, *P. hederaceum* Schott (= *P. jacquinii* Schott)

Grex *Belocardium* Schott: *P. hoffmannii* Schott, *P. advena* Schott, *P. acrocardium* Schott

Grex *Cardiobellium* Schott: (no species represented)

Grex *Meconostigma* Schott: (no species represented)

Grex *Eubelium* Schott: (no species represented)

Grex *Macrolonchium* Schott: (no species represented)

Grex *Macrobelium* Schott: *P. daemonum* Liebm. = *P. sagittifolium* Liebm., *P. sagittifolium* Schott, *P. tanyphyllum* Schott = *P. sagittifolium* Liebm.

Grex *Imbéa*: (no species represented)

Grex *Oligophlebium* Poepp.: (no species represented)

Grex *Doratophyllum* Schott: (no species represented)

Grex *Schizophyllum* Schott: (no species represented)

Grex *Tritomophyllum* Schott: *P. tripartitum* (Jacq.) Schott, *P. dagilla* Schott = *P. tripartitum* (Jacq.) Schott, *P. anisotomum* Schott

Grex *Polytomium* Schott: *P. subincisum* Schott, *P. impolitum* Schott = *P. radiatum* Schott, *P. polytomum* Schott = *P. radiatum* Schott, *P. warszewiczii* K. Koch & Bouché

Grex *Sphincterostigma* Schott: (no species represented)

In all, only 18 of the 135 species of *Philodendron* included in this 1860 revision were from Central America, and 4 of the total were members of *P.* grex *Pteromischum*. One of the four species, *P. ligulatum* Schott, is a member of *P.* sect. *Philodendron*, which Schott had inadvertently placed in his grex *Pteromischum*. Five of Schott's names became *P. hederaceum* (*P. acrocardium*, *P. hoffmannii*, *P. oxycardium*, *P. scandens*, and *P. micans*), but the count was reduced by only four since the name *P. hederaceum* was involved in two currently accepted species (namely, *P. hederaceum* and *P. jacquinii*). Other reductions are *P. gracile*, which is a synonym of *P. tenue*; *P. daemonum* and *P. tanyphyllum*, which are synonyms of *P. sagittifolium*; *P. dagilla*, a synonym of *P. tripartitum*; and *P. impolitum* and *P. polytomum*, synonyms of *P. radiatum*. Thus Schott was dealing with only 16 (16.5%) of the 96 currently known Central American species.

ADOLF ENGLER

Little was done with *Philodendron* following Schott's death in 1865 until Adolf Engler, working at the Universities of Kiel and Breslau (and finally at the Berlin Botanical Garden), began his revisionary work on the Araceae. Schott had laid the groundwork, describing most of the genera that still exist today, but he was dealing with only a small portion of the species. Taking up his first positions at Kiel and Breslau in 1871, at age 27, Engler worked with various tropical families on the *Flora Brasiliensis* project, publishing and working on a general review of the vegetative and floral morphology for the entire family (Engler, 1877). Later, in his powerful position as Director of the Berlin Botanical Garden, Engler commanded attention and a wealth of herbarium specimens and living material from all over the world during Germany's preeminent period of domination in the botanical world preceding World War II. Since Engler was only 21 at the time of Schott's death, it is not likely that the two ever met, but Engler would have had access to some of the same material, including living material from the Schönbrunn greenhouses, as well as Schott's notes and illustrations made over a 40-year period (Engler, 1876). Unlike modern workers, he had access to Schott's herbarium in Vienna before it was destroyed during World War II. This is important for a continuum of species concepts in groups often described from inadequate material of unknown origin and worse yet sometimes destroyed by war.

Engler's (1878) treatment of the Araceae in Martius's *Flora Brasiliensis* included 116 species of *Philodendron*, 95 of which were members of *P.* sect. *Philodendron* (13 were in *P.* sect. *Pteromischum* and 8 in *P.* sect. *Meconostigma* (Schott) Engl.). Only 47 species of *Philodendron* were then known from Brazil. The work also included sectional and species descriptions as well as a key to all existing species of *Philodendron*. In this work Engler modified Schott's system of classification for *Philodendron* by recasting Schott's "greges" as sections and reducing the number from 22 to 10. He also synonymized a number of species, reducing the total from 132 to 116 species. Only a single Central American species, *P. oxycardium* (= *P. hederaceum* var. *oxycardium*) was reported for Brazil, a fairly accurate picture as we know today. Only a couple of other species, namely *P. fragrantissimum* and *P. verrucosum*, have been found to range into the Am-

azon drainage of South America. Two additional species, *P. glanduliferum* Matuda and *P. brevispathum*, have a subspecies or variety that occurs in the Amazon basin of South America, but the same do not occur in Central America.

In the following year Engler's treatment of *Philodendron* for A. and C. DeCandolle's *Monographie Phanerogamarum* (Engler, 1879) was essentially unchanged, adding only 3 species to bring the total to 120. Of these, 93 species were members of *P.* subg. *Philodendron* and 20 of the epithets represented species currently known from Central America (now reduced to 15 through synonymy).

The final revisionary effort by Engler on *Philodendron* published 20 years later (Engler, 1899) was changed only slightly at the subgeneric level from the 1878 work. One section was raised to subgeneric status, and the remaining nine sections were included in *P.* subg. *Euphilodendron* Engl. (now *P.* subg. *Philodendron*). Despite minor changes made by Krause (1913), it is essentially Engler's classification that persists almost a century later. Engler's (1899) revision was substantially larger than Schott's last revision. Engler's revision contained 167 species, 134 of them in *P.* subg. *Philodendron*, with 23 reported for Central America (reduced to 15 species through synonymy in this revision). One species, *P. purpureoviride* Engl., reported for Ecuador, is now known for Central America.

The species of *P.* subg. "*Euphilodendron*" included in Engler's (1899) revision broken down by section for Central America are listed below:

P. sect. *Pteromischum* Schott: *P. aurantiifolium* Schott (as synonym of *P. guttiferum* Kunth), *P. guatemalense* Engl., *P. inaequilaterum*, *P. seguine*, *P. talamancae* Engl.

P. sect. *Baursia* (Rchb. ex Schott) Engl.: *P. wendlandii* Schott

P. sect. *Polyspermium* Engl.

"Gruppe" *Platypodium* Schott: *P. pterotum*

"Gruppe" *Solenosterigma* Klotzsch: *P. oxycardium* (= *P. hederaceum* var. *oxycardium*), *P. purpureoviride* (as *P. purpureoviridis* from South America), *P. micans* K. Koch (= *P. hederaceum* var. *hederaceum* forma *micans*), *P. scandens* (= *P. hederaceum* var. *hederaceum*)

"Gruppe" *Cardiobelium* Schott: *P. brevispathum*, *P. gracile* (= *P. tenue*), *P. schottianum*, *P. tenue*

"Gruppe" *Achyropodium* Schott: *P. verrucosum*

P. sect. *Oligospermium* Engl.

"Gruppe" *Macrobelium* Schott: *P. sagittifolium*, *P. daemonum*, *P. sanguineum* Regel (= *P. sagittifolium*), *P. mexicanum* Engl.

"Gruppe" *Belocardium* Schott: *P. ligulatum* Schott, *P. advena*, *P. subovatum* Schott (= *P. advena*), *P. smithii* Engl.

"Gruppe" *Oligocarpidium* Engl.: *P. pittieri* Engl. (= *P. hederaceum*)

P. sect. *Tritomophyllum* (Schott) Engl.: *P. anisotomum*, *P. tripartitum*, *P. fenzlii* Engl. (= *P. tripartitum*)

P. sect. *Schizophyllum* (Schott) Engl.: no species represented

P. sect. *Polytomium* (Schott) Engl.: *P. augustinum* K. Koch (= *P. radiatum*), *P. radiatum* Schott, *P. warszewiczii* K. Koch & Bouché

P. sect. *Macrolonchium* (Schott) Engl.: *P. fragrantissimum*

P. sect. *Macrogynium* Engl.: *P. hoffmannii* Schott sensu Engl. (= *P. jacquinii* Schott)

The turn of the century saw major activity with *Philodendron*, no doubt due to Engler's just published revision. Engler made no changes in his revision but went on to publish 26 additional species (Engler, 1905b). In addition, seven species were described by Alfred Barton Rendle, Ignaz Urban, Ambroise Gentil, and N. E. Brown between 1901 and 1908.

KURT KRAUSE

Kurt Krause, who began working with Engler at the Berlin Botanical Garden on 1 January 1905, described two additional species before preparing his revision of *Philodendron* for *Das Pflanzenreich* (Krause, 1913). The latter remains the most recent revision of the whole genus. Krause's revision is a slightly reworked version of Engler's (1899) revision but did include the description of a new section, *P.* sect. *Camptogynium*, with a single species in *P.* subg. *Philodendron* ("*Euphilodendron*") and included 55 more species. There were 32 other new species published in *P.* subg. *Philodendron*. Six of these were in *P.* sect. *Pteromischum* (*P.* subg. *Pteromischum*), while one was in *P.* subg. *Meconostigma*. The remaining 25 were in *P.* subg. *Philodendron*. Most were members of *P.* sect. *Baursia* and *P.* sect. *Polyspermium* (*Philodendron*) with a single species each in the following sections: *Oligospermium* (*Calostigma*), *Schizoplacium*, *Macrolonchium*; and three species in *P.* sect. *Polytomium*. Only two species, *P. grandipes* K. Krause and *P. panamense* K. Krause (both in current *P.* sect. *Philodendron*), were from Central America. Krause's treatment of *P.* subg. *Philodendron* included the following sections and species for Central America (or at least now known from Central America):

Names used by Krause (1913) and their current status. Species numbers refer to those in Krause's revision.

2. *P.* sect. *Baurea* (Rchb. ex Schott) Engl.
   39. *P. wendlandii* Schott
3. *P.* sect. *Polyspermium* Engl.
   67. *P. coeruleoviride* Engl. (member of *P.* subg. *Pteromischum* mistakenly placed here)
   70. *P. pterotum* K. Koch & Augustin
   77. *P. grandipes* K. Krause
   90. *P. purpureomaculatum* Engl. (reported for Ecuador)
   95. *P. scandens* K. Koch & Sello = *P. hederaceum*
   96. *P. oxycardium* Schott = *P. hederaceum* var. *oxycardium*
   99. *P. micans* K. Koch = *P. hederaceum* var. *hederaceum* forma *micans*
   108. *P. schottianum* H. Wendl. ex Schott
   110. *P. panamense* K. Krause
   117. *P. gracile* Schott = *P. tenue* K. Koch & Augustin
   116. *P. tenue* K. Koch & Augustin
   125. *P. verrucosum* L. Mathieu ex Schott
4. *P.* sect. *Oligospermium* Engl.
   134. *P. sagittifolium* Liebm.
   140. *P. sanguineum* Regel = *P. sagittifolium* Liebm.
   147. *P. mexicanum* Engl.
   150. *P. ligulatum* Schott
   164. *P. subnudum* Schott = *P. sagittifolium* Liebm.
   168. *P. smithii* Engl.
   173. *P. advena* Schott
   176. *P. pittieri* Engl. = *P. hederaceum* (Jacq.) Schott
5. *P.* sect. *Tritomophyllum* (Schott) Engl.:
   181. *P. fenzlii* Engl. = *P. tripartitum* (Jacq.) Schott
   182. *P. anisotomum* Schott
   183. *P. tripartitum* (Jacq.) Schott
6. *P.* sect. *Schizophyllum* (Schott) Engl.: (no species represented in Central America).[1]
7. *P.* sect. *Polytomium* (Schott) Engl.:
   195. *P. radiatum* Schott
   198. *P. augustinum* K. Koch = *P. radiatum* Schott
   199. *P. polytomum* Schott = *P. radiatum* Schott
   200. *P. wurszewiczii* K. Koch & Bouché
8. *P.* sect. *Macrolonchium* (Schott) Engl.
   202. *P. fragrantissimum* (Hook.) Kunth
9. *P.* sect. *Macrogynium* Engl.
   207. *P. hoffmannii* Schott sensu Engl. = *P. jacquinii* Schott
10. *P.* sect. *Campogynium* K. Krause: (no species represented in Mesoamerica)

The 28 Central American species names for *Philodendron* subg. *Philodendron* represented only 11% of the 222 species in Krause's revision. Of the 28 taxa Krause reported for Central America, *P. coeruleoviride* was a member of *P.* subg. *Pteromischum*, 19 are now considered synonyms of other Central American species which he also reported or which have been subsumed into other species as varieties or subspecies. Of the ten, two, *P. tenue* and *P. jacquinii*, have been given older names that he did not report but still represent Central American species. Thus, Krause's revision of *Philodendron* of Central America treated only 19 species, roughly ½, of the total currently known for Central America. One additional Central American species, *P. purpureomaculatum*, was treated by Krause but not reported for Central America.

Modern Work

Since no revisionary work took place on *Philodendron* between the time of Krause and the advent of *Philodendron* specialist George Bunting's (1963a) revisionary work, most species were described as the result of floristic work and most of these were from South America. In all, 142 new species epithets for *Philodendron* have been introduced to date since the time of Krause's revision (including 5 species published by Grayum, 1992b). In addition, 11 new varieties, 7 new subspecies, and 1 new form were published during this period. Six new combinations were made. Of this total only 33 species of *Philodendron* were reported for Central America, and 11 of these were in *P.* subg. *Pteromischum*. Thus 22 species of *P.* subg. *Philodendron* were published between the last full revision of the genus by Krause and the completion of the current work (not including those species of *P.* subg. *Pteromischum* in Grayum (1996)). The Mesoamerican taxa of *P.* subg. *Philodendron* described between the time of Krause's revision and the completion of this work are as follows: *Philodendron apocarpum* Matuda (= *P. jacquinii* Schott), *P. auriculatum* Standl. & L. O. Williams, *P. basii* Matuda, *P. brenesii* Standl., *P. davidsonii* Croat, *P. dressleri* G. S. Bunting, *P. erlansonii* I. M. Johnst. (= *P. jacquinii*), *P. glandulliferum* Matuda, *P. harlowii* I. M. Johnst. = *P. hederaceum*, *P. jamapanum* G. S. Bunting (= *P. sagittifolium* Liebm.), *P. jo-*

[1] *Philodendron petiolatum* (Hook.) Kunth was reported by John Hall of Costa Rica but no live or dried material is available for confirmation.

dariense G. S. Bunting, *P. lancigerum* Standl. & L. O. Williams (= *P. sagittifolium*), *P. latisagittum* Matuda (= *P. mexicanum*), *P. lundellii* Bartlett ex Lundell (= *P. jacquinii*), *P. microstictum* Standl. & L. O. Williams, *P. miduhoi* Matuda = *P. hederaceum*, *P. mirificum* Standl. & L. O. Williams (= *P. pterotum* K. Koch & Augustin), *P. monticola* Matuda = *P. advena*, *P. platypetiolatum* Madison, *P. pleistoneurum* Standl. & L. O. Williams (= *P. grandipes* K. Krause), *P. pseudoradiatum* Matuda (= *P. radiatum* var. *pseudoradiatum* (Matuda) Croat), and *P. trisectum* Standl. (= *P. anisotomum*).

Three additional species were described in *Philodendron* but actually pertain to other genera (see under "Excluded Names").

Many of the other taxa in Krause's revision were synonymized or reduced in rank, and only 11 taxa in *P.* subg. *Philodendron* remained. These were: *P. brenesii*, *P. radiatum* var. *pseudoradiatum*, *P. auriculatum*, *P. microstictum*, *P. basii*, *P. glanduliferum*, *P. dressleri*, *P. jodavisianum*, *P. platypetiolatum*, *P. davidsonii*, and *P. strictum*.

Most of the Central American floristic work outside of Mexico was carried out by Paul C. Standley, often working with his associate Louis O. Williams. Standley worked initially at the Smithsonian and later at the Field Museum in Chicago, then at the herbarium of the Escuela Agrícola Panamericana, where he died at Zamorano in Honduras. Standley described *P. brenesii* and *P. trisectum* (= *P. anisotomum* Schott) alone, and with L. O. Williams he also provided the following epithets: *P. armigerum* (= *Syngonium armigerum* (Standl. & L. O. Williams) Croat), *P. auriculatum*, *P. brevinodum* (= *Monstera tuberculata* Lundell var. *brevinoda* (Standl. & L. O. Williams) Madison), *P. hastiferum* (= *Syngonium hastiferum*), *P. lancigerum* (= *P. sagittifolium*), *P. microstictum*, *P. mirificum* (= *P. pterotum*), and *P. pleistoneurum* (= *P. sagittifolium*). It is unusual that despite the fact that there were many undescribed species of *Philodendron* subg. *Philodendron* in Costa Rica and Panama, these workers did not succeed in describing many of them since of the nine described, three proved to belong to other genera, and three others proved to be synonyms of existing *Philodendron* names. This is particularly surprising since both Standley and L. O. Williams were astute observers who were very familiar with the Central American flora in general. Their mistakes point out the complexity of the taxonomy of Araceae and the bewildering array of material available to them at that time. Even when I began my own work with the Araceae in the late 1960s there were few specimens (aside from types) that proved to have the correct names. Specimens were often poorly preserved and inadequate, and virtually all lacked good field notes. Either field observations or well-prepared field notes describing aspects of the plants not available on dried plants are essential to the proper understanding of *Philodendron* and other Araceae. I believe that it is possible that this confusion, coupled with the dearth of well-prepared specimens and the paucity of types of Araceae, discouraged workers from making decisions about which species were new.

Perhaps owing to the difficulty with the genus, local floras in Central America were often inadequately done, even if one considers that fewer specimens were available to the authors than today. The treatment of the *Flora of Panama* (Standley, 1944), for example, is woefully inadequate considering the small percentage of the total aroid flora that is covered compared to what is now known to exist.

In his treatment of some genera Standley (1944) seemed too willing to accept epithets of species described in Colombia, regardless of how well they "fit" Panamanian species. As a result many species names in genera such as *Anthurium*, for example, were wrong. His treatment of *Philodendron* subg. *Philodendron* was much better from the standpoint of correct names, but he treated only 8 of the 104 taxa (7%) of *Philodendron* subg. *Philodendron* now known for Panama. Only one species, *P. hoffmannii* (now *P. jacquinii*), had the wrong name. *Philodendron jacquinii* was also misapplied, being intended by Standley for *P. hederaceum*. The other species he included in the *Flora of Panama* were: *P. brenesii*, *P. brevispathum*, *P. grandipes*, *P. panamense*, *P. radiatum*, *P. tripartitum*, and *P. wendlandii*. He did not do so well with members of *P.* subg. *Pteromischum*, where *P. karstenianum* Schott was a mixture of two species and *P. guttiferum* was a mixture of three species. Perhaps the most curious thing about Standley's *Flora of Panama* treatment is that by 1944, after Robert Woodson and his collaborators had already made several expeditions to Panama, so few of the new species included in the present revision had been collected. Standley had collected some of the new species but failed to recognize them as new. These included: *P. crassispathum* (*Standley & Valerio 51910*), *P. findens* (*Standley & Torres 52355*), *P. purulhense* (*Standley 89902*), *P. strictum* (*Standley 51371*), *P. verapazense* (*Standley 91978*), and *P. wilburii* var. *wilburii* (*Standley 38300*). See discussion of those species for additional details. See also section on "Collecting History of *P.* subg. *Philodendron*."

The *Flora of Guatemala* (Standley & Steyermark, 1958b) was much more accurate and complete in the percentage of the total taxa of *P.* subg. *Philo-*

dendron included. However, this probably has less to do with the fact that it was published 14 years later than it does with the fact that there are fewer, generally more widespread species occurring there than in Panama. *The Flora of Guatemala* treated 11 species of *Philodendron*, 8 of them members of *P.* subg. *Philodendron*. These were: *P. anisotomum*, *P. hederaceum*, *P. hoffmannii* (= *P. jacquinii*), *P. radiatum*, *P. sagittifolium*, *P. smithii*, *P. tripartitum*, and *P. warszewiczii*. With 50% of the present total taxa included and with all but one of the taxa still properly bearing the name, the Guatemala treatment remains generally more useful than that of the *Flora of Panama*. Added to the flora since the 1958 revision are: *P. advena*, *P. fragrantissimum*, *P. glanduliferum*, *P. jodavisianum*, *P. mexicanum*, *P. purulhense*, and *P. verapazense*.

The *Flora of Guatemala* (Standley & Steyermark, 1958b) treated *P. hederaceum* correctly but treated *P. jacquinii* under its synonym, *P. hoffmannii*. Curiously, however, the illustration used represents both species. The leaf and stem seem clearly to be *P. hederaceum*, but the inflorescence clearly shows the long-protruded styles of *P. jacquinii*.

Standley's (1937) treatment of the Araceae of Costa Rica was reasonably good, partly because many species had been described by Schott from collections made by H. Wendland in Costa Rica. Other widespread species whose taxonomy had been well established were also a part of the flora. Properly named Costa Rican species recognized by Standley were: *P. brenesii*, *P. ligulatum*, *P. pterotum*, *P. radiatum*, *P. schottianum*, *P. tripartitum*, *P. verrucosum*, and *P. wendlandii*. Species now synonymized are: *P. gracile* (= *P. tenue*), *P. hoffmannii* (= *P. jacquinii*), *P. pittieri* (= *P. hederaceum*), and *P. trisectum* Standl. (= *P. anisotomum*). It has never been determined which species he included under the name *P. panamense*, but that species is not known for Costa Rica. Thus, with 8 out of the 13 names correct and 3 additional species that at least represent synonyms of currently recognized species, Standley did pretty well. However, with only 13 of the current 49 species treated (26%), the treatment was no more complete than that of the *Flora of Panama*, which was written a few years later.

Though no other floristic taxonomist had such a prominent role with Central American *Philodendron* as Standley, there were others who described *Philodendron* during the course of their floristic work.

Ivan M. Johnston of the Arnold Arboretum described *Philodendron erlansonii* (= *P. jacquinii*) and *P. harlowii* (= *P. hederaceum*) while working on the flora of San José Island (Johnston, 1949) of Panama.

In Mexico, Eizi Matuda, the local aroid specialist, described seven species (Matuda, 1954): *P. apocarpum* (= *P. jacquinii*), *P. basii*, *P. glanduliferum*, *P. latisagittium* (= *P. mexicanum*), *P. miduhoi* (= *P. hederaceum*), *P. monticola* (= *P. advena*), and *P. pseudoradiatum* (= *P. radiatum* var. *pseudoradiatum*); and George Bunting described four species during his investigations of Mexican Araceae (Bunting, 1965): *P. dressleri*, *P. jamapanum* (= *P. advena*), *P. jodavisianum*, and *P. tuxtlanum* G. S. Bunting (= *P. sagittifolium*).

Matuda's treatment of the *Philodendron* in Mexico (Matuda, 1954) dealt with 16 species, 13 of them in *P.* subg. *Philodendron*. While a number of the species had the correct names, e.g., *P. advena*, *P. mexicanum*, *P. pseudoradiatum*, *P. radiatum*, and *P. tripartitum*, others had synonymous names, e.g., *P. sanguineum* and *P. daemonum* (both currently recognized as *P. sagittifolium*). Matuda also recognized *P. mexicanum* under three different names, namely *P. mexicanum*, *P. latisagittatum*, and *P. sagittifolium* (a distinct species that he treated as both *P. daemonum* and *P. sanguineum* (a currently recognized name improperly used; see above). Matuda redescribed two species using the names *P. apocarpum* and *P. miduhoi* (currently *P. jacquinii* and *P. hederaceum*, respectively). Finally, he described *P. monticola* (now considered synonymous with *P. advena*).

Other Central American species of *P.* subg. *Philodendron* published since the time of Krause's revision and prior to the beginning of this project in 1986 are *P. davidsonii* and *P. platypetiolatum*, the latter described from Ecuador during Mike Madison's extensive work with the flora of Ecuador during his tenure at the Selby Botanical Garden. Thus, up to the initiation of the current study, only 26 species in *P.* subg. *Philodendron* were described for Central America. With 96 species of *P.* subg. *Philodendron* now known for Central America, this registers an increase of 70 species or a 270% increase.

Of the species of *P.* subg. *Philodendron* described since Krause's revision (not including the present effort) only seven were described by nonspecialists (I. M. Johnston, P. C. Standley, and Standley and L. O. Williams). Standley, together with L. O. Williams, described most of the new Central American species and wrote most of the floristic treatments of the Araceae for Central America. Despite his extensive experience, I do not believe that Standley fully understood the diversity of the Araceae. This is because he failed to recognize a rel-

atively large number of species that were new to science. In Standley's defense it must be stated that the Araceae are a particularly complex family with so much interspecific variation that proper decisions often cannot be easily made without direct comparisons of living material. In addition, collections in the past often had few or no field notes to use for study.

COLLECTING HISTORY

In addition to the history of revisionary efforts it is instructive to consider the collecting efforts in Central America that have laid the groundwork for the scientific work done with *Philodendron* subg. *Philodendron.* Perhaps owing to their sometimes intimidating size, the difficulty of retrieval, and certainly due to the difficulty of preparing and drying specimens, members of *P.* subg. *Philodendron* have never been popular with botanical collectors. The early neotropical collectors, i.e., Ruiz and Pavon, Sessé and Moçiño, Triana and Planchon, and others collected few Araceae (or at least few survived to modern times). Eduard Poeppig, working in Peru, and Richard Spruce, working in the Amazon region of Brazil, did somewhat better, collecting a number of new species. In Central America few collectors made many collections until modern times. Even Standley and Julian A. Steyermark, two of the most prodigious collectors in the region, did not make many collections of Araceae. Both gathered well over 100,000 collections in their careers. Yet in all, Standley made only 146 collections of *P.* subg. *Philodendron,* comprising 21 species in all of Central America. Of this total only 6 of the collections (these previously mentioned) proved to be undescribed species, none of which Standley recognized as new. Standley was not avoiding collecting *Philodendron* because they constituted a lot of work to press. This is demonstrated by the fact that he collected *P. radiatum* 13 times and *P. warszewiczii* 12 times. These are among the most difficult plants to prepare owing to their huge size and fleshy parts.

That so few new species of *Philodendron* were collected was apparently due to the fact that in earlier times relatively few roads led into areas of wet forest.

Matuda, working exclusively in Mexico and concentrating on Araceae, accrued 27 collections of *P.* subg. *Philodendron* and only 1 of these, *P. glanduliferum,* proved ultimately to be new to science. George Bunting, also working only in Mexico (under the numbers of Harold Moore of Cornell University), made 36 collections of *P.* subg. *Philodendron,* including 2 new species (*P. dressleri* and *P. jodavisianum*).

Steyermark, though collecting many more *Philodendron* in Venezuela later in his career, collected only 26 Central American *P.* subg. *Philodendron,* comprising 9 species, none of which were new. L. O. Williams, who also worked on the *Flora of Guatemala* and collected for many years in Guatemala, Honduras, and Costa Rica, made only 14 collections of *P.* subg. *Philodendron.* Two of these were species that remained undescribed until this work, namely *Williams 628* (*P. sulcicaule*) and *Williams 28387* (*P. wilburii* var. *longipedunculatum* Croat & Grayum). Percy Gentle, collecting in Belize, made 20 collections. The *Philodendron* subg. *Philodendron* collections of Pittier in Costa Rica totaled nine, none representing new species. Adolf Tonduz, also working in Costa Rica, made only five collections of this group. Alberto Brenes made four collections in Costa Rica between 1926 and 1932. Two of them, *P. brenesii* and *P. bakeri,* proved to be new. Paul Allen made five collections of *Philodendron* in Costa Rica, four of which were described as new (though two were subsequently synonymized). Aside from these few collections of new species mentioned above, no other new species were collected until the early 1960s. Roy Lent, living in Costa Rica and collecting between 1964 and 1971, made 24 collections of *P.* subg. *Philodendron,* including 5 new taxa. These are: *P. lentii* Croat & Grayum, *P. hederaceum* var. *kirkbridei, P. strictum, P. thalassicum* Croat & Grayum, and *P. wilburii* var. *wilburii.* W. C. Burger, collecting in Costa Rica between 1968 and 1986, in part with one-time aroid specialist Richard Baker, made 56 collections of *P.* subg. *Philodendron,* including 5 new species, *P. bakeri, P. chirripoense, P. crassispathum, P. thalassicum,* and *P. wilburii.*

Though Panama is even richer in Araceae than Costa Rica, the collecting activity there was not particularly rewarding. The *Philodendron* collections of H. von Wedel, who worked in Bocas del Toro Province in Panama, totaled only seven. Robert Woodson and his collaborators, Paul Allen, and Carrol Dodge collectively made only 11 collections before the *Flora of Panama* project was begun. This occurred in a country that proved to have 96 species, 65 new to science.

Even James Duke, who regularly got into areas of wet forest in many parts of Panama, made only four collections of *P.* subg. *Philodendron,* none of them new.

Collecting activities begun by Walter H. Lewis and staff from the Missouri Botanical Garden in the early 1960s were more aggressive by using heli-

copters, and made it into areas not previously accessible. Despite this greater penetration, even these expeditions resulted in few specimens of *Philodendron*. John Dwyer, one of the principal participants in these early Panama expeditions (and later Belize), made 14 collections of *Philodendron* (mostly from Panama), 2 of which [*P. dwyeri* (from Belize) and *P. stramineicaule* Croat)] were new to science. During the same period, Edwin Tyson, while teaching for Florida State University in the former Canal Zone, made 16 collections, 5 of them new to science: *P. annulatum* Croat & Grayum, *P. dolichophyllum* Croat, *P. lasseri* Croat, *P. llanense* Croat, and *P. tysonii* Croat. Even the late Alwyn Gentry, who made more than 80,000 collections of tropical American plants during his career and who went to many remote and interesting areas, made only 24 collections of *P.* subg. *Philodendron* in Central America. Three of them, *P. llanense*, *P. pseudauriculatum*, and *P. wilburii*, were undescribed at the time.

Collecting in Honduras, Costa Rica, and Panama between 1973 and 1993, Ron Liesner collected 43 species of *P.* subg. *Philodendron*, 4 of them, *P. alticola* Croat & Grayum, *P. crassispathum*, *P. findens*, and *P. llanense*, new to science.

Michael Grayum, an aroid specialist working primarily with *P.* subg. *Pteromischum*, was involved personally or in conjunction with other collectors, in making (since 1984) 426 *Philodendron* collections (in both Central and South America). Of this total, 153 were of *P.* subg. *Philodendron* for Central America. His collections are particularly useful, since they are accompanied by excellent field notes. He was responsible for collecting 13 undescribed species of *P.* subg. *Philodendron*: *P. angustilobum* Croat & Grayum, *P. aromaticum* Croat & Grayum, *P. bakeri*, *P. brunneicaule* Croat & Grayum, *P. colobrusense*, *P. crassispathum*, *P. cretosum* Croat & Grayum, *P. dodsonii* Croat & Grayum, *P. grayumii* Croat, *P. scalarinerve* Croat & Grayum, *P. stramineicaule*, *P. thalassicum*, and *P. wilburii*.

My own collecting activities with *Philodendron* began in 1967 with work on the *Flora of Barro Colorado Island* (Croat, 1978). Collecting on BCI and taking other trips in Panama with Walter Lewis, John Dwyer, and others gave me my first real experience gathering Araceae. Many of the areas visited were not previously explored by botanists, mostly in wet or very wet areas where numerous new Araceae occurred. Many species were collected for the first time even in areas where considerable collecting had been carried out in the past. In some cases nearly all the species collected on a given day proved to be new to science. Later, when serving as the Missouri Botanical Garden's resident botanist in Panama, during 1970–1971, and while continuing my work on Barro Colorado Island, I took many field trips to other areas of Panama. By this time I had become seriously interested in collecting Araceae, and many plants were brought back to Summit Garden for cultivation and study. Upon my return to St. Louis, most of these collections were shipped to the Missouri Botanical Garden where many have persisted. In all, 3582 collections of *Philodendron* have been made by myself (or sometimes in conjunction with another collector) in Central and South America; 1715 of these were made in Central America, and 1594 of these were members of *P.* subg. *Philodendron*: these Central American collections represented 52 undescribed species.

FOSSIL HISTORY

The fossil history of the Araceae was reviewed recently by Grayum (1990). The records are scant and inconclusive, but macrofossils of Araceae showed the family to be relatively diverse by the early Tertiary (Daghlian, 1981; Gregor & Bogner, 1984), and at least four modern subfamilies were present by the Oligocene. No fossil pollen definitely ascribed to *Philodendron* has yet been encountered (Grayum, 1990). A plant fossil from Tennessee believed to be a *Philodendron*, and described as *P. limnestis* Dilcher & Daghlian (Dilcher & Daghlian, 1977), has proven to be a member of Peltandreae, either *Peltandra* or *Typhonodorum* (J. Bogner, pers. comm.). This fossil was believed by the authors to be a member of *P.* subg. *Meconostigma*. Mayo (1991) discussed in detail why he believed that it could not be a *Philodendron*, instead comparing it most closely with *Typhonodorum*.

INTRAGENERIC RELATIONSHIPS

The last thorough taxonomic revision of the Araceae was that by Engler (1905–1920), conducted in part by K. Krause (Engler & Krause, 1908, 1920; Krause, 1913). That revision included eight subfamilies of Araceae with *Philodendron* in its own subfamily and tribe, Philodendroideae and Philodendreae, respectively. Philodendreae (Engler, 1911) shared the subfamily with seven other tribes, namely, Schismatoglottidinae, Anubiadeae, Aglaonemateae, Dieffenbachieae, Zantedeschieae, Typhonodoreae, and Peltandreae. Engler (1912) grouped *Philodendron* with *Homalomena* and the genera of the largely Asian subtribe Schismatoglottidinae (*Bucephalandra*, *Gamogyne*, *Microcasia*, and *Piptospatha*) into subtribe Philodendrineae.

Bogner and Nicolson (1991) left Engler's subfamily Philodendroideae intact, but Grayum (1984) made substantive changes including an incorporation of the subfamily Calloideae and the Calocasioideae (thus forcing a change in the subfamilial name to Calloideae, because of nomenclatural priority). The subfamily is divided into *Nephthytis*, *Aglaonema*, *Peltandra*, and *Philodendron* Alliances. In Grayum's system, *Philodendron*, in its own tribe Philodendreae, originally shared the alliance with the tribes Spathicarpeae, Dieffenbachieae, and Bognereae. Both *Dieffenbachia* and *Bognera* are in their own tribes, but the Spathicarpeae have eight small genera mostly occurring in southern South America: *Asterostigma*, *Gearum*, *Gorgonidium*, *Mangonia*, *Spathantheum*, *Spathicarpa*, *Synandrospadix*, and *Taccarum*. Grayum (1990) later placed *Philodendron* close to Homalomeninae and the African genera *Culcasia* and *Cercestis* (which had been placed in the Pothoideae and Lasioideae, respectively, by Engler). They all share similar stem and stamen vasculature as well as extrafloral nectaries and resin canals in their roots and a sclerotic root hypodermis. Most (excluding Homalomeninae) also lack an anther endothecium that is present in all other Araceae (Grayum, 1990). Grayum believed that the Philodendroideae are a sister group to the Pothoideae (including Engler's Monsteroideae), which have in common the exclusive characteristics of geniculate petioles, cork formation in aerial roots, compound vascular bundles, collateral bundles, and other features (Grayum, 1984).

While there is reasonable agreement on the classification of tribes and subtribes, subfamilial concepts are still evolving. A comparison of the major systems of classification at the suprageneric level was made by Croat (1990[1992]). It included the systems of Hotta (1970), Grayum (1990), and Bogner and Nicolson (1991).

Phenetic analysis on the Philodendroideae by Mayo (1986) shows *Philodendron* to be distinct but without any definitive diagnostic features with which to distinguish it completely from other genera. He reported the genus to be only distantly related to other genera in the subfamily but that its closest relatives were the African genera *Culcasia* and *Cercestis*. In his survey of sclerotic hypodermis in the roots of Araceae, French (1987a) provided evidence to link *Philodendron* to the West African genera *Anubias*, *Culcasia*, and *Cercestis* and the neotropical *Montrichardia*.

More recently, in an attempt to bridge differences in the systems of Bogner and Nicolson, Grayum, and Hay and Mabberley (1991), Mayo et al. (1995) conducted another sweeping survey and produced a cladistic analysis. While maintaining essentially the same alliances suggested by Grayum (1990), Mayo et al. (1995) placed all araceous genera with unisexual flowers in subfamily Aroideae. *Philodendron* is placed in tribe Philodendreae in the *Philodendron* Alliance, along with tribe Homalomeneae with *Furtadoa* and *Homalomena* and tribe Anubiadeae (*Anubias* only). Their cladistic analysis also shows *Bognera* to be a close ally of *Dieffenbachia*.

Another cladistic analysis resulting from a study of chloroplast DNA restriction site variation in the Ariflorae by French et al. (1995) places *Philodendron* as a sister group to *Homalomena*, suggesting, according to Grayum (1996), that Homalomeninae is paraphyletic. According to French's findings, *Anubias* is a sister taxon of *Homalomena*, *Furtadoa*, and *Philodendron* taken together, while *Montrichardia* is a sister taxon to all four of these genera.

While questions still remain about the closest generic relatives of *Philodendron*, the classification by Mayo et al. (1995) has taken into account all the evidence to date including the extensive molecular studies by French.

The genera of Araceae most easily confused with *P.* subg. *Philodendron* are *Homalomena* and *Dieffenbachia*, with *Schismatoglottis* coming a distant third. Despite the somewhat more distant placement of *Dieffenbachia* from *Homalomena*, herbarium material of *Dieffenbachia* is most easily confused with *Philodendron*, sometimes requiring the opening of the spathe to determine the genus. Since the pistillate flowers of *Dieffenbachia* are distant from one another, surrounded by clavate staminodia and borne on a spadix that is fused throughout its length to the spathe, while those of *Philodendron* are closely compacted, devoid of staminodia, and borne on a spadix that is largely free from the spathe, separation from *Dieffenbachia* is immediate as long as the flowers are visible. Dried sterile material without field notes denoting terrestrial habit (consistently true of *Dieffenbachia*, but rarely so of *Philodendron*) or scent (usually foul and of oxalic acid in *Dieffenbachia*) are much more problematic. *Dieffenbachia* leaf blades are rarely ovate and never truly cordate, whereas this blade shape is common in *Philodendron*. *Philodendron* may, however, have blade shapes that closely match those of some *Dieffenbachia*. If the petiole is well preserved the presence of the petiole sheath is the best means to separate *Dieffenbachia* and *P.* subg. *Philodendron*; the latter generally has a very short sheath, while it is rare that the sheath of *Dieffenbachia* does not extend to the middle or above the middle of the petiole.

Live material of neotropical *Homalomena* is not easily confused with *Philodendron* because the for-

mer usually has anise-scented sap, while *Philodendron* usually has a distinct turpentine-like aroma, sometimes also like fresh carrots, but never anise-scented. *Philodendron* and *Homalomena* may have similar leaves, but the latter often has pubescence on the blades and pubescence and/or scales and spines on the petioles. These two genera have similar inflorescences with unisexual flowers, sterile and fertile sections of the staminate portion of the spadix, and a close arrangement of pistillate flowers, not to mention the similar constricted spathe that persists after anthesis. However, *Homalomena* can usually be determined by the presence of minute, club-shaped staminodia sparsely scattered among the pistils.

Sterile specimens of neotropical *Schismatoglottis* may be confused with *Philodendron* by the novice because the two genera share similar venation. However, *Schismatoglottis* always occurs terrestrially, often in somewhat marshy situations where *Philodendron* rarely occurs. In fertile condition they are easily separated by the spathe promptly dehiscing above the tube in *Schismatoglottis,* with the staminate portion of the spadix falling free. By contrast, in *Philodendron* the spathe is thick and persistent, usually reclosing over the staminate portion of the spadix, which in turn rots away inside, never really falling free until the spathe opens in fruit.

Sterile material of *Spathiphyllum* has been confused with *Philodendron,* but that genus differs by its consistently terrestrial habit, long-sheathed petioles (exhibited in *Philodendron* only in *P.* subg. *Pteromischum*), the presence of trichoscherieds, and by its distinctive, closely spaced primary lateral veins.

Infrageneric Relationships

Philodendron is currently divided into three subgenera. A subgeneric system of classification for *Philodendron* was proposed as early as 1832 by Schott, who recognized four unranked groups: *Euphilodendron, Calostigma, Meconostigma,* and *Sphincterostigma.* The latter two were combined by Engler (1899) as *P.* subg. *Meconostigma.* Schott's *Calostigma* was later called *P.* sect. *Oligospermium* Engl. (Engler, 1878) and is once more called *P.* sect. *Calostigma* [(Schott) Pfeiffer] (Mayo, 1990). *Euphilodendron* became *P.* sect. *Polyspermium* in Engler's *Flora Brasiliense* treatment in 1878 and must now be treated according to the Code (Greuter et al., 1994) as *P.* sect. *Philodendron* (Mayo, 1990).

It was not until Kunth's (1841) treatment that members of what are now called *P.* subg. *Pteromischum* were removed from *Monstera* and placed in *Philodendron.* Schott recognized *Pteromischum* as a grex in his 1860 *Prodromus,* and Engler first recognized the species occurring in this group as *P.* sect. *Pteromischum* in his *Flora Brasiliensis* treatment (Engler, 1878).

Phylogenetic and phenetic analyses by Mayo (1986, 1988) have shown *Philodendron* to have three subgenera distinct in vegetative and floral morphology, floral anatomy, and to some extent by distribution. *Philodendron* subg. *Meconostigma,* with a predominantly southeastern South American distribution, is highly apomorphic but cladistically primitive in the genus (Mayo, 1990). Based on a study of gynoecial morphology Mayo considers *P.* subg. *Meconostigma* to have evolved in eastern Brazil as a group adapted to open habitats and later spread into the more humid Amazon basin. By the same standard he assumed that *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* also arose later and became predominant as hemiepiphytes in humid forests. He considered *P.* subg. *Pteromischum* to be a sister group to *P.* subg. *Philodendron* and that *P.* subg. *Philodendron* is the most advanced of the three subgenera. The geological history of the continent would probably support this since eroded mountain plateaus of eastern Brazil are much older than the current land surfaces of the Amazonian basin. Most of the species of the genus, now so rich on the Andean slopes of northern and western South America, surely must have evolved since the Andes arose during the late Cenozoic.

Mayo elevated *P.* sect. *Pteromischum* to the status of subgenus (Mayo, 1989) and Grayum (1996) subdivided the subgenus into two sections, *P.* sect. *Pteromischum* (Schott) Engl. with sylleptic[4] sym-

[4] *Sylleptic shoots* are shoots that develop from lateral meristems without any cessation of activity after initiation, i.e., growth is continuous with the lateral shoot usually taking over from the main axis, which terminates in flowering in most Araceae genera. *Sylleptic sympodial growth,* characteristic of *P.* subg. *Philodendron,* results when branching occurs from a non-resting lateral bud such that the existing stem with its terminal inflorescence is immediately overtopped by continued growth of the axillary branch in a manner that makes it appear that the growth of the stem is indeterminate and that the inflorescences produced appear to be axillary to the leaf produced by the new stem segment. This type of growth, though in reality a series of branches, each with a single cataphyll (prophyll of Ray), a single stem segment, and a single leaf (sympodial foliage leaf of Ray; metaphyll of Grayum) and terminated by an inflorescence, appears to be an unbranched stem producing a continuous series of cataphylls, and a continuous series of what appears to be laterally attached leaves each with an axillary inflorescence (see fig. 3 in Ray, 1987b).

podial growth and *P.* sect. *Fruticosa* Grayum with proleptic[5] sympodial growth (Ray, 1987b), a growth form that is rare in the family, known only in *Alocasia* and a few species of *Monstera* (Grayum, 1996).

Philodendron subg. *Philodendron* is difficult to define and is primarily distinguished by its negatives, i.e., it lacks the specific characteristics of *P.* subgenera *Pteromischum* and *Meconostigma* (see key to subgenera below). There are relatively few members of *P.* subg. *Philodendron* with a pachycaulous habit common to so many members of *P.* subg. *Meconostigma*, i.e., with very stout, generally erect stems and possessing conspicuous leaf scars. *Philodendron* subg. *Philodendron* also lacks the conspicuous, more or less triangular scales borne in the leaf axils of *P.* subg. *Meconostigma*. Though sometimes obvious (Fig. 11) in *P.* subg. *Philodendron*, they are usually small and inconspicuous and fall early. The species most similar to *P.* subg. *Meconostigma* is *P. warszewiczii*, but another species, *P. basii*, is similar in being large with a thick, erect stem.

Species of *P.* subg. *Pteromischum* have subtle characteristics that to the expert permit immediate recognition. These characters include the slender, somewhat woody, brittle stem, a conspicuous petiole sheath, thinner blades with rather pronounced primary lateral veins, the presence of interprimary veins, and the frequent presence of raphide cells or stitch-like markings. Another feature that is often useful in separating *P.* subg. *Pteromischum* from *P.* subg. *Philodendron* is the much higher incidence of asymmetrical leaf blades in the former. Species with asymmetrical (especially at the base) blades are not common in *P.* subg. *Philodendron*. Some species of *P.* subg. *Philodendron* may have oblong to elliptic, non-cordate blades like those of *P.* subg. *Pteromischum*, but they never have the fully sheathed petioles of the latter (except in juvenile condition, which may confuse the non-expert).

The three subgenera of *Philodendron* in general can be most easily separated by the characters presented in the following key (modified after Mayo, 1991).

KEY TO THE SUBGENERA OF *PHILODENDRON*

1a. Stem of mature flowering plants with a succession of many leaves terminated by a solitary or commonly several inflorescences; petioles with long sheaths narrowly encircling the stem at their base ..... *P.* subg. *Pteromischum*

1b. Stem of mature flowering plants with a succession of short sympodial segments each bearing a cataphyll and a single leaf with the inflorescence(s) 1 to many and appearing to be borne in the leaf axils; petioles of adult plants with short, usually inconspicuous petiole sheath and borne on the side of the stem, not encircling it at the base.

2a. Stems often arborescent; staminodial zone between staminate and pistillate zones of the spadix subequal or longer than fertile zone; stamens usually at least 3 times longer than broad ..... *P.* subg. *Meconostigma*

2b. Stems rarely arborescent, often scandent; staminodial zone between staminate and pistillate zones of spadix much shorter than the fertile staminate zone; stamens less than 3 times longer than broad ..... *P.* subg. *Philodendron*

There are also a number of anatomical characteristics separating the subgenera. Vegetative buds of *Philodendron* subg. *Philodendron* are always located below the point of overlap in the sheath margins of the cataphyll, whereas they are lacking in *P.* subg. *Pteromischum* (Ray, 1987b). *Philodendron* subg. *Pteromischum* is distinct in having a style with a shallow compitum[6] with a subepidermal concentration of raphide crystals (Mayo, 1986, 1989) and a total lack of tannin cells in the stamens (Mayo, 1986). In addition, while hypophyllous[7] stem segments are typical for *P.* subg. *Philodendron* they are ambiphyllous,[8] hyperphyllous,[9] or peraphyllous[10] in *P.* subg. *Pteromischum*. *Philodendron* subg. *Philodendron* is characterized by having continuous parenchyma from the cortex to the center of the stem. In contrast, *P.* subg. *Pteromischum* has a central cylinder with a solid ring of fibers around it.

While not definitive, there are a number of other features that normally are useful to separate *P.*

[5] *Proleptic sympodial growth*, characteristic of members of *Philodendron* sect. *Fruticosa* (Grayum, 1996), results when branching occurs from a bud that has rested, relative to the parent shoot, so that the lateral branch does not appear until well after the inflorescence has set fruit and fallen off. Thus the inflorescence appears to be terminal, not axillary as in sylleptic sympodial growth. The first few internodes in proleptic growth are very short, lack buds, and produce a consecutive series of cataphylls or reduced leaves (see fig. 2 in Ray, 1987b).

[6] The common depression that leads to individual stylar canals.

[7] Hypophyllous stem segments are those those in which the petiole scar borders the lower edge of the segment (see figs. 3, 7 in Ray, 1987b).

[8] Ambiphyllous stem segments are so short that the petiole scars border on both ends of the stem segment (see figs. 9–11 in Ray, 1987b).

[9] Hyperphyllous stem segments have the petiole scar at the upper edge of the stem segment (see figs. 2, 8 in Ray, 1987b).

[10] Peraphyllous stem scars are those in which the internode subtending the petiole "is elongated and supercedes the point of attachment" (Ray, 1987b).

subg. *Pteromischum*. Its blades are typically more or less oblong, moderately thin, and typically more inequilateral than those of *P.* subg. *Philodendron*. The stems of *P.* subg. *Pteromischum* are commonly less than 1 cm in diameter and frequently with rather long internodes. While there are many members of *P.* subg. *Philodendron* with more or less oblong leaf blades, blades of most species are cordate or subcordate at the base. Many members of *P.* subg. *Pteromischum* have stems that branch and spread away from their support before flowering; this behavior is rare in *P.* subg. *Philodendron*.

Because of the usually conspicuously sheathed petioles of *P.* subg. *Pteromischum*, the subgenus is more likely to be confused with sterile specimens of *Rhodospatha* than with the oblong-bladed species of *P.* subg. *Philodendron* (and in such cases the presence of trichosclereids beneath the epidermis of *Rhodospatha* easily distinguishes it from *Philodendron*).

Relationships within *P.* subg. *Philodendron*

Discussion of subgeneric classification. Any attempt to revise the subgeneric classification of *Philodendron* subg. *Philodendron* is frustrated by the lack of morphological characteristics that correlate with one another throughout the subgenus. Engler (1899) separated the species of *P.* subg. *Philodendron* primarily on the basis of leaf shape, leaf blade venation, and the nature of the pistil (i.e., number of locules per ovary, type of placentation, and number of ovules per locule). Most sections, all moderately small ones, were separated on the basis of leaf morphology. These are: *P.* sect. *Tritomophyllum*, *P.* sect. *Schizophyllum*, and *P.* sect. *Polytomium*. Two sections, *P.* sect. *Macrogynium* and *P.* sect. *Camptogynium*, are based on the nature of the pistil. Following a cladistic analysis of a relatively small number of species, including some in *P.* subg. *Philodendron*, Mayo (1986) concluded that *Philodendron* should be divided into two to three sections instead of the existing nine sections in the genus. While I agree that *P.* sect. *Macrolonchium* should be reduced, I think that a cladistic analysis making use of the leaves as well would justify the existence of the remaining sections recognized by Krause with the possible exception of *P.* sect. *Camptogynium*, which was not studied by Mayo.

The most time-honored way to separate species in *P.* subg. *Philodendron* is based on number of ovules per locule, a system first devised by Engler stemming from his first revision of *Philodendron* (Engler, 1878). Engler used the number of ovules per locule to separate two large groups, which he called *P.* sect. *Polyspermium* and *P.* sect. *Oligospermium* (now *P.* sect. *Philodendron* and *P.* sect. *Calostigma*, respectively). These two sections together comprise the largest percentage of species in the subgenus. As they are constituted they are very diverse morphologically, and it is possible that the number of ovules per locule will not prove to be reliable for separation at the sectional level. It is possible that species with relatively few ovules or solitary ovules may have evolved independently several times from ancestors with numerous ovules having axile placentation. Since it has not yet been determined if this is the case, the classification system used here will in general be conservative.

Krause (1913) closely followed Engler's sectional revision. His *P.* sect. *Philodendron* (as *P.* sect. *Polyspermium*) consisted of species with axile placentation and "many" ovules per locule, while *P.* sect. *Calostigma* (as *P.* sect. *Oligospermium*) consisted of those species with sub-basal (or less frequently basal) placentation with "1 or few" ovules per locule. Since the time of the last revision of *Philodendron* many species have been added, and the distribution of ovules per locule for all species now forms a more complete continuum. There is still a significant correlation between axile placentation and moderately large numbers of ovules per locule and the converse, basal and sub-basal placentation and relatively low numbers of ovules. Both *P.* sect. *Philodendron* and *P.* sect. *Calostigma* will be discussed below.

While these two groups, *P.* sect. *Philodendron* and *P.* sect. *Calostigma*, constitute the largest percentage of Central American species, several other sections are separated on the basis of leaf shape, venation, and style type (see above key). Each of these will be discussed in turn, despite the fact that some do not occur in Central America. Krause (1913) treated ten sections in his revision of *Philodendron*. As previously discussed, *P.* sect. *Pteromischum* has been elevated to the status of subgenus, and *P.* subg. *Macrolonchium* Engl. has been reduced to a subsection of *P.* subg. *Philodendron*.

1. **Philodendron** sect. **Baursia** (Rchb. ex Schott) Engl., in Mart., Fl. bras. 3(2): 134. 1878. *Philodendron* grex *Baursia* Rchb. ex Schott, Syn. Aroid. 73. 1856. TYPE: *Philodendron crassinervium* Lindl. (lectotype, designated by Mayo, 1990).

As defined by Engler and Krause, *P.* sect. *Baursia* consists of species with generally inconspicuous primary lateral veins, but the group as constituted

by Krause remains highly variable in terms of its ovules, habit, and leaf shape. The group comprises species with moderately many ovules and axile placentation, moderately many ovules with basal placentation, a few ovules with basal placentation, and solitary ovules with basal placentation. All of these species have leaves purportedly devoid of primary lateral veins. In reality this is not true of all species included in the group. Most species have elongate, simple blades, but three have 3-lobed or tripartite blades.

With 33 species included by Krause the section was third in size of the three major sections (*P.* sect. *Philodendron* with 64 and *P.* sect. *Calostigma* with 53 species). One species, *P. acreanum* K. Krause, is actually a member of *P.* sect. *Pteromischum.* Of the remaining species in the section, those that best fit the description of the group occur principally in eastern South America and in the upper Amazon basin and have more or less oblong leaf blades. *Philodendron crassinervium* is the type of the section. Except for *P. crassinervium, P. longilaminatum* Schott (with axile placentation), *P. bahiense* Engl., and *P. paxianum* K. Krause (each with solitary ovules per locule), species of *P.* sect. *Baursia* have a few basal ovules per locule and oblong to oblong-elliptic blades. Many but not all have indistinct primary lateral veins.

Some members of Krause's *P.* sect. *Baursia,* especially the species that are vines with a solitary ovule per locule and occur in the Andes west of the Continental Divide, such as *P. lehmannii* Engl., *P. ellipticum* Engl., *P. pachycaule* K. Krause, *P. chimboanum* Engl., *P. longipes* Engl., and *P. graveolens* Engl., do not seem to belong with the remainder and should perhaps be put into another section. The same is true of the three-lobed and tripartite species, *P. deltoideum* Poepp. & Endl., *P. panduriforme* (Kunth) Kunth (Krause also included here *P. reichenbachianum* Schott, now a variety of *P. panduriforme*), and *P. micranthum* Poepp. ex Schott. With the exception of *P. micranthum,* which has primary lateral veins lacking or weak, these species have primary lateral veins at least some of the time (though they are indistinct in *P. deltoideum*). None of the three species appear to have any other features in common with the more typical members of *P.* sect. *Baursia,* e.g., *P. crassinervium* Lindl., *P. linnaei* Kunth, and *P. callosum* K. Krause, among others.

Mayo (1986) believed that *P.* sect. *Baursia* contained two groups of species, and he would also separate *P. deltoideum* and related species from the remainder, suggesting that Schott's grex *Oligophlebium* be recognized to accommodate these species.

Some species that were placed in *P.* sect. *Baursia* will have to be reinvestigated to determine if they belong instead in *P.* sect. *Philopsammos* G. S. Bunting (1986). That group is often similar in having elongated leaf blades, but it differs in having bilocular ovaries whereas those of *P.* sect. *Baursia* are plurilocular.

By no means all of the species with more or less oblong blades in *P.* sect. *Baursia* have primary lateral veins weak or lacking. At least one species, *P. wendlandii,* the only Central American species placed in *P.* sect. *Baursia* by Engler, should be placed in *P.* sect. *Calostigma.* It has distinct primary lateral veins and a spongiose petiole with a distinct dark green annular ring like the other members of *P.* subsect. *Glossophyllum* in Central America. This leaves Central America without members of *P.* sect. *Baursia.*

2. Philodendron sect. **Philopsammos** G. S. Bunting, Phytologia 60: 306. 1986. TYPE: *Philodendron ptarianum* Steyerm., Fieldiana, Bot. 28: 99. 1956. [*Philodendron callosum* K. Krause subsp. *ptarianum* (Steyerm.) G. S. Bunting, Phytologia 64: 467. 1988.]

Philodendron sect. *Philopsammos* is restricted to South America, known largely from the region of the Guiana highlands with extensions into the Amazon basin, occurring principally on white sand savannas, sandstone outcrops, and on tepuis, rarely in alluvium in lowland forests. It is characterized by having usually terrestrial or epipetric, thick, creeping stems with mostly short internodes, mostly long persistent, mostly intact cataphylls, moderately long petioles, mostly erect, geniculate petioles, more or less oblong, elliptic to narrowly ovate, coriaceous blades, usually lacking any prominent posterior lobes and with usually distinct, sometimes moderately obscure primary lateral veins. Inflorescences are moderately large with pistils bilocular, rarely 3-locular, and ovaries moderately numerous with axile placentation.

Included in the section are the following species: *P. canaimae* G. S. Bunting, *P. craspedodromum* R. E. Schult., *P. dunstervilleorum* G. S. Bunting, *P. dyscarpium* R. E. Schult., *P. peraiense* G. S. Bunting, *P. phlebodes* G. S. Bunting, *P. pimichinense* G. S. Bunting, *P. callosum* K. Krause, *P. pulchrum* G. M. Barroso, *P. remifolium* R. E. Schult., *P. sabulosum* G. S. Bunting, *P. steyermarkii* G. S. Bunting, and *P. tatei* K. Krause. Perhaps also to be included

in this group is *P. englerianum* Steyerm. No species in the group occur in Central America.

In describing this section Bunting (1986) made no mention of how the section is distinguished from *P.* sect. *Baursia* (or any other section). This is a critical point since both sections have species with elongated blades and at least sometimes have primary lateral veins not markedly more prominent than the interprimary veins (secondary lateral veins). The section is presumably distinguished from *P.* sect. *Baursia* on the basis of having mostly two locules per ovary. As an indication of its affiliation with *P.* sect. *Baursia,* Bunting, at the time he described *P.* sect. *Philopsammos,* specifically mentioned *P. callosum* (a species included by Krause in *P.* sect. *Baursia* and initially considered by Bunting to be distinct from *P. ptarianum*) as being a possible member. *Philodendron ptarianum* has proven to be closely related to *P. callosum,* but that species was described by Krause as being "plurilocula," i.e., with many locules per ovary and "pauciovulata," i.e., with few ovules per locule. If this is true, the single character separating *P.* sect. *Philopsammos* from *P.* sect. *Baursia,* namely the small number of locules per ovary, would break down even in two subspecies (as now recognized by Bunting, 1995), one of which is the type of *P.* sect. *Philopsammos.* One collection of *P. callosum, Davidse & Miller 27269,* had 2-locular ovaries with 8–10 ovules per locule with unusual black, shiny seeds. It would clearly appear to be a member of *P.* sect. *Philopsammos.*

3. Philodendron sect. **Philodendron.** TYPE: *P. grandifolium* (Jacq.) Schott

Philodendron sect. *Philodendron* in Central America is both large and diverse, and like *P.* sect. *Calostigma* (a discussion of which follows) it is further subdivided here into subsections.

With 38 species (40 taxa) *P.* sect. *Philodendron* is the second largest section in *P.* subg. *Philodendron* in Central America. *Philodendron* sect. *Philodendron* is characterized by having axile placentation and typically many ovules per locule but, owing to its size and diversity, there are no other characters that completely characterize the group. *Philodendron* sect. *Polyspermium* (according to the Code (Art. 21) it must now be *P.* sect. *Philodendron*) was subdivided by Krause into six groups, "Gruppen" (termed subsections by Mayo, 1990). These subsections will be discussed here, especially in relation to the Central American species.

SUBSECTIONS OF *P.* SECT. *PHILODENDRON*

1. Philodendron subsect. **Macrolonchium** (Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *Philodendron* grex *Macrolonchium* Schott, Prodr. syst. Aroid. 269. 1860. TYPE: *Philodendron simsii* (Hook.) G. Don (lectotype, designated by Mayo, 1990: 64).

This is a small group of species characterized by D-shaped or broadly and sharply sulcate petioles and the presence of short stems with short internodes. The leaf blades typically are ovate-triangular. The cataphylls typically persist as fibers. The ovaries are 5–10-locular with numerous ovules per locule. This group was treated by Engler (1899) and Krause (1913) as a section based on stems with internodes shorter than broad versus scandent stems, but the group is in no way warranted at the sectional level based on this or any other character.

Though neither short stems nor D-shaped petioles are unique to this group, it appears to be natural at the subsectional level. All of the species have similar ovate-triangular blades and coarse reddish brown persistent cataphyll fibers. The two pinnately lobed species in the group, *P. pinnatifidum* (Jacq.) Schott and *P. robustum* Schott, seem unlikely members of this subsection. Those species are very similar to *P. fendleri* K. Krause, which Engler placed in his *P.* sect. *Polytomium. Philodendron pinnatifidum* and *P. robustum* should probably be placed there as well. They seem to have little in common with the other simple-leaved species. *Philodendron melinonii* Brongn., *P. fragrantissimum, P. simsii,* and *P. roraimae* K. Krause all appear to be related. The only Central American species in this subsection is *P. fragrantissimum.*

2. Philodendron subsect. **Canniphyllum** (Schott) Mayo, J. Linn. Soc., Bot. 100. 168. 1989. *Philodendron* grex *Canniphyllum* Schott, Syn. Aroid. 76. 1856. TYPE: *Philodendron fibrillosum* Poepp.

This is a small group that included only five species in Krause's revision and one of these, *P. coerulescens,* proved to be a synonym of *P. inaequilaterum,* a member of *P.* subg. *Pteromischum. Philodendron juninense* Engl., *P. fibrillosum,* and *P. cuneatum* Engl. are all Andean species, while the no doubt distantly related *P. blanchetianum* Schott is a species from eastern Brazil in Bahia. *Philodendron* subsect. *Canniphyllum* has only a few species in Central America. Both *Philodendron cretosum* and *P. roseospathum* have persistent fibrous cataphylls and resemble the type species, *P. fibril-*

losum (selected by Mayo, 1990). The only other Central American species that has characteristics to fit in the subsection is *P. chirripoense*, which is tentatively placed here, though it differs in having longer, more slender internodes and lacks persistent cataphylls. The presence or absence of persistent cataphylls is highly correlated with the length of internodes (persistent when internodes are short, deciduous when internodes are long) and thus it is not surprising that *P. chirripoense* would lack cataphylls. Still, the latter is a most peculiar species so its placement remains in doubt.

3. Philodendron subsect. **Platypodium** (Schott) Engl., in Mart., Fl. bras. 3: 137. 1878. *Philodendron* grex *Platypodium* Schott, Syn. Aroid. 85. 1856. TYPE: *Philodendron pterotum* K. Koch & Augustin (lectotype, designated by Mayo, 1990: 61).

This group was characterized by Schott (1856) as having D-shaped petioles. While he included both *P. pterotum* and *P. fragrantissimum*, Engler later transferred the latter to his *P.* sect. *Macrolonchium* (Schott) Engl. Mayo (1990) designated the only remaining species in Schott's section, namely *P. pterotum*, as the type species.

In addition to *P. pterotum*, Krause (1913) placed in *P.* sect. *Platypodium* four more species, *P. clementis* Wright, now considered a synonym of *P. fragrantissimum* (a member of *P.* subsect. *Macrolonchium*); *P. splitgerberi* Schott, a possible synonym of *P. fragrantissimum*; *P. lechlerianum* Schott, a close relative of *P. purpureoviride* (a member of *P.* subsect. *Solenosterigma*); and *P. ernestii* Engl. Thus, of the species listed by Krause, probably only *P. pterotum* and *P. ernestii* belong here. It is unlikely that *P. ernestii* is very closely related to *P. pterotum*, but it does appear to be closely related to *P. brunneicaule*, another species placed in this section.

In addition to *P. pterotum*, other species of *P.* subsect. *Platypodium* that occur in Central America are: *P. brunneicaule*, *P. copense*, *P. findens*, and *P. fortunense* Croat.

4. Philodendron subsect. **Psoropodium** (Schott) Engl., in Mart., Fl. bras. 3: 138. 1878. *Philodendron* grex *Psoropodium* Schott, Syn. Aroid. 84. 1856. TYPE: *Philodendron ornatum* Schott (lectotype, designated by Mayo, 1990: 61).

As defined by Schott (1856), this is a group that has petioles verrucose at the apex. Mayo (1991) appropriately selected *P. ornatum* as the lectotype. Krause's description, "petioles semirounded above, smooth or asperous, blade base cordate or sagittate," would accommodate more than half of the species in the genus *Philodendron*, but Schott's intention for the subsection was clear. The only other species included by Schott was *P. rubens* Schott, now considered by some authors to be a synonym of *P. ornatum*. Krause also expanded the group substantially, adding a number of plants that do not have glandular petioles and others that have proven to be synonyms of *P. ornatum*. The latter are: *P. muschlerianum* K. Krause, *P. dolosum* Schott, *P. asperatum* K. Koch, and *P. tobagoense* Engl. The aberrant elements which, I believe, are unrelated to *P. ornatum* include *P. brevilaminatum* Schott and *P. traunii* Engl. (now both synonyms of *P. fragrantissimum* in *P.* subsect. *Macrolonchium*), *P. grandipes*, and *P. maximum* K. Krause, a gigantic species from the southwest Amazon basin that is unlikely to be related in any way to *P. ornatum*. I have moved *P. grandipes* from *P.* subsect. *Psoropodium* to *P.* subsect. *Philodendron*, where it more appropriately belongs.

Krause also included in his *Psoropodium* group three other poorly known species, *P. thaliifolium* Schott, *P. brandtianum* K. Krause, and *P. bertae* K. Krause. These do not appear to be in any way related to *P. ornatum*. It is clear from these as well as the other species included by Krause that the section as defined by Engler and by Krause no longer resembles Schott's original description. Probably a number of the species will need to be moved into other groups, or the section will need to be more well defined. As currently defined no species in *P.* subsect. *Psoropodium* occur in Central America.

5. Philodendron subsect. **Solenosterigma** (Klotzsch ex Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *Philodendron* grex *Solenosterigma* Klotzsch, Syn. Aroid. 81. 1856. TYPE: *Philodendron scandens* K. Koch & Sello [(= *Philodendron hederaceum* (Jacq.) Schott (lectotype, designated by Mayo, 1990: 61)].

As treated by Krause (1913), this appears to be a natural group, consisting of *P. hederaceum*, the type, as well as *P. consanguineum* Schott and a number of relatives. *Philodendron fuertesii* K. Krause, *P. krebsii* Schott, and *P. urbanianum* K. Krause all closely resemble *P. consanguinem*, and *P. marginatum* Urb., *P. prieurianum* Schott, *P. oxycardium*, *P. micans*, and *P. melanochrysum* Linden & André are all synonyms or subspecies of *P. hederaceum*. These species share long, slender inter-

nodes, deciduous, mostly unribbed cataphylls, more or less terete petioles, ovate-cordate leaf blades, and solitary inflorescences.

Other species included by Krause in *P.* subsect. *Solenosterigma* are *P. purpureoviride* (aside from *P. hederaceum* and *P. brevispathum*, the only other species of the group that occurs in Central America), *P. jenmanii* K. Krause, and *P. scabrum* K. Krause. The latter two species are now considered synonyms of *P. muricatum* Willd. ex Schott. Though surely belonging in *P.* subsect. *Solenosterigma* (along with the two synonyms already placed here) Krause placed *P. muricatum* in *P.* sect. *Calostigma*.

Philodendron brevispathum is transferred here from *P.* subsect. *Cardiobelium* (Schott) Engl., since it appears to be closely related to *P. muricatum*.

6. **Philodendron** subsect. **Philodendron**

Philodendron grex *Cardiobelium* Schott, Syn. Aroid. 88. 1856. *Philodendron* subsect. *Cardiobelium* (Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *Philodendron* "Gruppe" *Cardiobelium* (Schott) Engl., Bot. Jahrb. Syst. 26: 522, 529. 1899. TYPE: *Philodendron giganteum* Schott (lectotype, designated by Mayo, 1990: 60).

Philodendron grex *Eubelium* Schott, Syn. Aroid. 92. 1856. *Philodendron* subsect. *Eubelium* (Schott) Engl., in Mart., Fl. bras. 3: 140. 1878. TYPE: *Philodendron grandifolium* (Jacq.) Schott.

As defined by Schott (1860), grex *Cardiobelium* consisted of a single species, *P. giganteum*. The group was greatly expanded by Engler (1899) and by Krause (1913) as a subgroup within section *Polyspermium*. Now with 20 species, it constitutes the largest subsection in *P.* sect. *Philodendron*. The characterization, as expanded by Krause, "petioles smooth or lightly striate, asperate; blade cordate to sagittate, with the primary lateral veins much more conspicuous than the secondary veins," is so broad that many unrelated species might easily be contained within it. Certainly to be excluded is *P. rubens* Schott (now a synonym of *P. ornatum* and the core species in *P.* subsect. *Psoropodium*). Among the well known and seemingly distinct taxa included by Krause are *P. grandifolium*, *P. acutatum* Schott, and *P. fraternum* Schott, all with deciduous cataphylls, and *P. tenue*, *P. schottianum*, and *P. panamense*, with persistent cataphylls. The type, *P. giganteum*, also has conspicuous persistent cataphylls. A particularly unusual species included by Krause is *P. quitense* Engl., with deeply three-lobed leaves. It is probably a synonym of *P. acuminatissimum* Engl. in *P.* subsect. *Doratophyllum*.

The only Central American species included in the section by Krause were: *P. brevispathum*, *P. panamense*, *P. schottianum*, and *P. tenue*. *Philodendron brevispathum*, with its scaly stems, is best accommodated with *P. muricatum* in *P.* subsect. *Solenosterigma*.

Philodendron subsect. *Philodendron* has 20 species in Central America. The size and diversity of *P.* subsect. *Philodendron* warrant the recognition of the five series presented below.

SERIES OF *P.* SUBSECTION *PHILODENDRON*

1. **Philodendron** ser. **Philodendron.** TYPE: *P. grandifolium* (Jacq.) Schott

The series is not known from Central America, but has several species in South America. This group is characterized by thick stems, deciduous cataphylls, subterete petioles, large ovate-triangular blades conspicuously lobed at the base, several inflorescences per axil, and 5–7-locular ovaries with many ovules per locule. In addition to the type, *P. acutatum* Schott, *P. billietiae* Croat, and *P. megalophyllum* Schott appear to be typical members of this group, having many ovules per locule, deciduous cataphylls, more or less terete petioles, and ovate-triangular leaf blades.

2. **Philodendron** ser. **Impolita** Croat, ser. nov. TYPE: *P. strictum* G. S. Bunting

Internodia brevia; cataphylla persistentia; petiolus teres vel D-formatus; lamina palida adaxialiter, glaucescens.

Etymology. From impolitus meaning unpolished, i.e., matte, in reference to the matte and pale lower blade surfaces.

Three Central American taxa, *P. hebetatum*, *P. strictum*, and *P. thalassicum*, and at least one additional undescribed species from South America belong in this group. It is characterized by having leaf blades dark to medium green above but very pale, almost white beneath and covered with a minute waxy covering making the surface matte. The species have relatively short internodes, persistent cataphylls that often dry yellowish or have patches of yellowish epidermis persistent (not always true for *P. thalassicum*). Petioles may be obtusely somewhat flattened to D-shaped and dry with a yellowish epidermis (not always true for *P. thalassicum*). Blades are ovate-cordate to ovate-triangular.

3. **Philodendron** ser. **Velvetina** Croat, ser. nov. TYPE: *P. gigas* Croat

Internodia brevia, maxime crassa; cataphylla D-formata, persistentia in fibris tenuibus; petiolus subteres; lamina ovata-cordata, bicolorata, velutina adaxiliter, impolita abaxialiter, 81–125 cm longa, 37–90 cm lata.

Etymology. From velutinus meaning velvet, referring to the velvety upper surfaces of the blades.

The subsection consists of a single species, *P. gigas,* in Central America but would also include *P. andreanum* Devansaye from northern Colombia. The group is characterized by its stout stems, short internodes, cataphylls that persist as thin fibers, subterete petioles, and especially by the very large, narrowly ovate-cordate blades, which are velvety and bicolored on the upper surface with the midrib and primary lateral veins paler, and paler and matte on the lower surface. Inflorescences range up to 7 per axil.

4. Philodendron ser. **Fibrosa** Croat, ser. nov. TYPE: *P. jodavisianum* G. S. Bunting

Internodia brevia, cataphylla persistentia ut fibrae; petiolus plerumque teres aut subteres; lamina ovato-cordata; pistilla cum placentatione axiali; loculi pluriovulati.

Etymology. Fibrosa = composed of separable fibers, in reference to the cataphylls persisting as fibers.

This represents the largest series in *P.* subsect. *Philodendron.* It is characterized by thick stems, short internodes, cataphylls that usually persist as a mass of fibers on the stem, usually subterete petioles, and more or less ovate-cordate blades. Pistils have axile placentation and many ovules per locule.

The following species of *P.* ser. *Fibrosa* occur in Central America: *P. alticola, P. antonioanum, P. breedlovei, P. chiriquense, P. dodsonii, P. grandipes, P. jodavisianum, P. lazorii, P. llanense, P. panamense, P. pirrense, P. purulhense, P. scalarinerve, P. schottianum,* and *P. tenue.* Of these a few are still doubtful. *Philodendron grandipes,* with a D-shaped petiole, and *P. jodavisianum,* with a U-shaped petiole, perhaps belong in *P.* subsect. *Platypodium* but also do not seem to be related to the species in that group. *Philodendron breedlovei,* which appears to lack persistent cataphylls (specimen very incomplete), is at odds with the other species but fits nowhere else. A few species are in related clusters within the series; for example, *P. lazorii* and *P. panamense* seem to be closely related as do *P. grandipes* and *P. jodavisianum.*

Grayum (pers. comm.) believes that *P. dodsonii* perhaps belongs with *P. pterotum* in *P.* subsect. *Platypodium.*

5. Philodendron ser. **Albisuccosa** Croat, ser. nov. TYPE: *P. albisuccus* Croat

Internodia brevia; succus albus, calcareus; cataphylla persistentia in fibris tenuibus pallidis; petiolus subteres; lamina ovato-cordata; inflorescentia solitaria; pistilla 5–6-locularia; loculi cum 18–20 seminibus.

Etymology. Albus = white; succus = juice, sap, in reference to the white sap of cut parts.

The series consists of a single species, *P. albisuccus,* characterized by having copious white sap, which turns chalky on drying. Only one other species in Central America, *P. cretosum,* shares this unusual feature. It may belong in the same series despite its linear to oblanceolate leaf blades. It currently is placed in *P.* subsect. *Canniphyllum.*

7. Philodendron subsect. **Achyropodium** (Schott) Engl., in Mart., Fl. bras. 3: 139. 1878. *P.* grex *Achyropodium* Schott, Syn. Aroid. 85. 1856. TYPE: *P. verrucosum* L. Mathieu ex Schott

This is a seemingly quite natural group characterized by scaly petioles. As defined by Schott (1856) it was represented only by the type, *P. verrucosum.* Krause (1913) included six species (one of which, *P. arcuatum* K. Krause, is a synonym of *P. brevispathum* in *P.* subsect. *Solenosterigma*). The others in the subsection are: *P. nanegalense* Engl., *P. pilatonense* Engl., and *P. gualeanum* Engl. (all of which, I believe, represent a single species), as well as *P. serpens* Hook. f. All but *P. verrucosum* were known only from South America. There are several other undescribed species in *P.* subsect. *Achyropodium* now known from South America.

Philodendron subsect. *Achyropodium* is largely restricted to the northern Andes and lower Central America (Costa Rica and Panama) but has one species, *P. verrucosum,* that ranges as far south as Peru. The subsection is represented in Central America by *P. glanduliferum* subsp. *glanduliferum, P. hammelii, P. malesevichiae, P. squamicaule, P. squamipetiolatum,* and *P. verrucosum.*

4. Philodendron sect. **Calostigma** (Schott) Pfeiffer, Nomencl. Bot. 2: 674. 1874. *P.* [rankless] b. *Calostigma* Schott, in Schott & Endl., Melet. Bot. 19. 1832. TYPE: *P. imbe* Schott

Philodendron sect. *Calostigma* is the largest section in Central America with 48 species comprising 52 taxa. It is characterized by having basal or subbasal placentation and typically solitary or few ovules per locule. Owing to its size and diversity, there are no other characters that completely characterize the group.

There are some differences between *P.* sect. *Philodendron* and *P.* sect. *Calostigma* in Central America that are statistically significant, even if not without exception. For example, 81% of those spe-

Table 1. Leaf blade breakdown by section. # = number of species.

	Blades entire								Blades not entire		
	With basal lobes				Lacking basal lobes						
	Cordate		Subcordate		Ovate		Oblong		Incised-lobate		
Section	#	% of sect.	#	% of sect.	#	% of sect.	#	% of sect.	#	% of sect.	Section total
Calostigma	28	56%	7	14%	1	2%	14	28%	0	0%	50
Macrogynium	1	100%	0	0%	0	0%	0	0%	0	0%	1
Philodendron	34	81%	3	7%	1	2%	3	7%	1	2%	42
Polytomium	0	0%	0	0%	0	0%	0	0%	3	100%	3
Tritomophyllum	3	38%	0	0%	0	0%	0	0%	5	63%	8

cies in *P.* sect. *Philodendron* have cordate blades, while only 7% have subcordate blades, and 12% lack posterior lobes. In contrast, *P.* sect. *Calostigma* has only 56% of its species with cordate blades, 14% have subcordate blades, and 30% lack posterior lobes. See Table 1 for a complete breakdown by section.

See other comparisons between *P.* sect. *Calostigma* and *P.* sect. *Philodendron* under sections entitled "Ovary Locule Number" and "Ovules Per Locule" as well as in Appendix 2, Technical Data on Pistils.

Philodendron sect. *Calostigma* was subdivided by Krause into five groups (termed subsections by Mayo, 1990). These subsections will be discussed here, especially in relation to the Central American species.

1. Philodendron subsect. **Macrobelium** (Schott) Engl., in Mart., Fl. bras. 3: 143. 1878. *P.* grex *Macrobelium* Schott, Syn. Aroid. 96. 1856. TYPE: *P. sagittifolium* Liebm.

Philodendron subsect. *Belocardium* (Schott) Engl., in Mart., Fl. bras. 3: 141. 1878. *P.* grex *Belocardium* Schott, Prodr. Syst. Aroid. 255. 1860. TYPE: *P. advena* Schott (lectotype, designated by Mayo, 1990).

As reported by Krause, *Philodendron* subsect. *Macrobelium* was the largest subsection in *P.* sect. *Calostigma,* with 22 species. It was poorly defined by Krause as consisting of species with somewhat spongy petioles, 6–12-locular ovaries with relatively few ovules per locule, and basal to sub-basal placentation. In addition (although not stated by Krause), the blades are all cordate, sagittate, or hastate. Although Krause described the subsection as having 2–5 ovules per locule, many more species have been added to the group since the last revision and several species that logically belong in *P.* subsect. *Macrobelium* have more than 10 ovules per locule, despite having sub-basal placentation.

Philodendron subsect. *Belocardium* must be synonymized with *P.* subsect. *Macrobelium* since *P. advena,* clearly a close relative of *P. sagittifolium,* was designated the lectotype of the former subsection, and Schott's definition of grex *Macrobelium* differs little from grex *Belocardium,* primarily since the blades are described as elongate-sagittate with 6–7 primary lateral veins instead of ovate-cordate blades with 3–4 primary lateral veins for grex *Belocardium.* As defined originally by Schott (1860), *P.* grex *Belocardium* comprised vining plants with ovate-cordate blades with the posterior rib mostly lacking and not at all naked along the sinus and bearing solitary inflorescences with 1–2 ovules per locule. The group consisted of *P. subovatum* Schott (= *P. advena*), *P. hoffmannii* (= *P. hederaceum*), *P. deviatum* Schott (= *P. jacquinii*), *P. advena, P. populneum* K. Koch, *P. erubescens* Linden, *P. jacquinii, P. lindenii* Schott, *P. acrocardium* Schott, and *P. consanguineum* Schott. Several of these species are now known to be synonyms of *P.* sect. *Oligocarpidium* or *P.* sect. *Macrogynium. Philodendron lindenii* would have better served as a lectotype for the group and, along with *P. erubescens, P. deviatum,* and *P. populneum,* might have to be formed into a group distinct from *P.* sect. *Belocardium.*

Engler (1913) synonymized Schott's grex *Glossophyllum* with *P.* "Gruppe" *Belocardium,* but the former group, as defined by Schott, appears to be distinct and will be resurrected in this work. It comprises more or less scandent plants with tumid petioles and more or less oblong blades that are frequently subcordate or cordulate at the base (see that section for more details).

Because of its size (28 species) and the diverse composition of the species comprising *P.* subsect. *Macrobelium,* it was deemed necessary to divide the subsection into four series. A discussion of the new series of *P.* subsect. *Macrobelium* follows.

1. Philodendron ser. **Macrobelium** (Schott) Croat, ser. nov. TYPE: *P. sagittifolium* Liebm.

Philodendron ser. *Macrobelium* is the largest group of species in *P.* subsect. *Macrobelium* and includes the type. *Philodendron* ser. *Macrobelium* is distinguished by having moderately coriaceous, cordate to sagittate blades with the basal posterior rib usually not naked or only weakly naked near its base. In addition, cataphylls are usually deciduous or only briefly persistent. Most of the species in the series have a strong resemblance to the widespread *P. sagittifolium*. All members have type D styles (see section on style type), relatively few ovules per locule (usually 1–5, rarely to 6, 7, or 8). In most cases the ovules are contained within a translucent or transparent ovule sac.

Central American representatives of *P.* ser. *Macrobelium* are: *P. advena, P. annulatum, P. aromaticum, P. coloradense, P. dwyeri, P. edenudatum, P. ferrugineum, P. grayumii, P. knappiae, P. mexicanum, P. platypetiolatum, P. sagittifolium, P. subincisum, P. sousae, P. verapazense,* and *P. zhuanum. Philodendron platypetiolatum* is unusual in having a much-flattened petiole. Perhaps it warrants recognition as a separate series.

Philodendron mexicanum, long considered a member of the group, is unusual in not greatly resembling *P. sagittifolium* and in having blades sometimes more or less hastate.

It is possible that *P. annulatum* belongs in *P.* subsect. *Glossophyllum* because it sometimes has a purple annular ring at the apex of the petiole (one of the features characterizing this subsection) and usually has only 1–2 ovules per locule (though sometimes 4–5 ovules per locule).

2. Philodendron ser. **Ecordata** Croat, ser. nov. TYPE: *P. brenesii* Standl.

Internodia elongata vel brevia; cataphylla decidua; petiola subteres; lamina acuta vel subcordata ad basim; nervia minores saepe "etched" in superficie supra; pistila 5–14 locularia; loculi plerumque 4–14 ovulati.

Philodendron ser. *Ecordata* represents a group of species with elongate stems, internodes often longer than broad, deciduous cataphylls, elongate petioles, and blades that are ovate to ovate-elliptic, acute, or at most subcordate at the base (hence the name "ecordata," meaning without a cordate blade), often with the minor veins on the upper surface weakly etched. The basal veins are either free to the base or if they are united into a posterior rib, the latter is not naked or is naked for only a short distance. Pistils are 5–14-locular and locules are 4–14-ovulate.

The Central American species of *P.* ser. *Ecordata* are: *P. brenesii, P. crassispathum, P. davidsonii, P. lentii,* and *P. niqueanum.* A relationship between *P. brenesii* and *P.* ser. *Impolita* is possible, based on the glaucous lower blade surface in *P. brenesii,* but no other member of the group has glaucous leaves. Moreover, all the members of the above group usually have internodes longer than wide and have deciduous, rather than persistent cataphylls.

3. Philodendron ser. **Reticulata** Croat, ser. nov. TYPE: *P. tysonii* Croat

Internodia brevia; cataphylla persistentia in fibris tenuibus; petiolus lamina subequans aut longior, teres aut subteres; lamina ovato-cordata; pistila cum loculis 5–9-ovulatis; ovulae plerumque 5–7 per ovaria.

Etymology. Reticulus, meaning netted, referring to the dried network of cataphyll fibers characterizing this series.

Philodendron ser. *Reticulata* is the only group of species in *P.* subsect. *Macrobelium* with a few ovules per locule, stems with short internodes, and persistent cataphylls. Most species with short internodes and persistent cataphyll fibers are members of *P.* sect. *Philodendron.* Species in this group have terete or subterete petioles about as long as the ovate-cordate blades and pistils with 5–9 loculles, each with 5–7 ovules.

Philodendron ser. *Reticulata* is represented in Central America by only two species, *P. jefense* and *P. tysonii.*

4. Philodendron ser. **Pachycaulia** Croat, ser. nov. TYPE: *P. basii* Matuda

Caudex succulentus; internodia brevia, crassa; cataphylla 2-costata, persistentia intacta; petiolus teres; lamina ovato-cordata, costae postice desnudae secus sinum ad 4 cm; pistila 4–6-locularia; loculi 4–6 ovulati.

Etymology. Pachy = thick, caule = stem, referring to the thick, succulent stems.

Philodendron ser. *Pachycaulia* is represented by a single species and is characterized by its very stout succulent stems with intact persistent cataphylls, terete petioles, ovate-cordate blades with the posterior rib naked along the sinus to 4 cm. The pistil has a type D style and is 4–6-locular with 4–6 ovules per locule. It is believed that the succulent stems evolved to store water, allowing the plant to survive the long dry season in western Mexico. The series is represented only by *P. basii* from western Mexico.

2. Philodendron subsect. **Glossophyllum** (Schott) Croat, comb. nov. Basionym: *Philodendron* grex *Glossophyllum* Schott, Syn. Aroid. 80. 1856. TYPE: *P. elaphoglossoides* Schott (lectotype, designated by Mayo, 1990).

1. Philodendron ser. **Glossophyllum** Croat, ser. nov. TYPE: *P. elaphoglossoides* Schott

Philodendron subsect. *Glossophyllum* consists of two new series, *Glossophyllum* and *Ovata.*

Philodendron ser. *Glossophyllum,* as defined here, has the appearance of being a natural group of species with more or less oblong leaves acute or frequently cordulate or subcordate at the base. The primary lateral veins are usually distinct. Stems are typically somewhat scandent, though some members of the group, such as *P. auriculatum, P. bakeri, P. dolichophyllum, P. ligulatum, P. morii, P. pseudauriculatum, P. utleyanum,* and *P. wendlandii,* sometimes have the internodes scarcely longer than broad. The petioles are usually spongy or subspongy, usually subterete, and often bear a purplish or greenish annulus around the circumference where the petiole joins the blade; the cataphylls may be unribbed or sharply 1–2-ribbed and are typically deciduous (though persisting for a time in some species with short internodes, e.g., *P. auriculatum* and *P. wendlandii*). The style type is variable in the group, with most having B or D type styles but with one species, *P. granulare,* having an unusual type E style. Many species in the series have orange berries. *Philodendron* ser. *Glossophyllum* ranges from Nicaragua to Colombia and Ecuador on the Pacific slope and to the Guianas and the Amazon basin.

Krause included this group of plants with his section *Belocardium,* comprising both Schott's grex *Belocardium* and grex *Glossophyllum.* The former group consisted of plants with elongate internodes and ovate-cordate to sagittate blades, and Krause included *P. subovatum* Schott (= *P. advena*), *P. lindenii* Schott, *P. weberbaueri* Engl., *P. smithii, P. subhastatum* Engl. & K. Krause, *P. myrmecophyllum* Engl., *P. pachyphyllum* K. Krause, *P. advena,* and *P. viride* Engl. The latter group included species with mostly oblong blades. He characterized his section *Belocardium* as having tumid petioles and unilocular ovaries. Most of the species in the cordate-bladed group are not believed to be closely related to *P.* ser. *Glossophyllum* and have been referred here to *P.* subsect. *Macrobelium* (see discussion of *P.* subsect. *Macrobelium*). What remains is a group that usually has more or less oblong blades with tumid petioles that are purple-ringed at the apex and ovaries usually unilocular.

Philodendron smithii, the only other Central American species among those mentioned above, does indeed have tumid petioles and only a single ovule per locule like most members of *P.* subsect. *Glossophyllum,* but the great difference in leaf shape in this species and others placed here warrant their separation into another series within *P.* subsect. *Belocardium* (see below).

Though Krause's revision characterized *P.* subsect. *Belocardium* as having a single ovule per locule, that is not in itself the defining feature of the subsection. For example, several species typical of the group have oblong leaves, purple-ringed petioles, and the same general appearance but have more than one ovule per locule. These are: *P. auriculatum,* with (3)4 ovules per locule; *P. ligulatum* var. *heraclioanum,* and *P. ligulatum* var. *ovatum,* both with 2; *P. pseudauriculatum,* with 1–2(4); and *P. wendlandii,* with 2. *Philodendron bakeri* sometimes has 2 ovules per locule. Other Central American species, each with 1 ovule per locule are *P. brewsterense, P. correae, P. dolichophyllum, P. folsomii, P. granulare, P. immixtum, P. ligulatum, P. morii, P. ubigantupense,* and *P. utleyanum.*

Typical South American species in *P.* subsect. *Glossophyllum* presented by Krause (1913) are: *P. cyrtocleum* Diels (= *P. ruizii* Schott), *P. longipetiolatum* Engl., *P. heterophyllum* Poepp., *P. uleanum* Engl., *P. adhatodifolium* Schott, *P. elaphoglossoides* Schott, *P. ruizii* Schott (erroneously placed in sect. *Baursia* by Schott), *P. wittianum* Engl., and *P. angustialatum* Engler. *Philodendron tenuipes* Engl., placed in *P.* subsect. *Belocardium* by Engler, appears to be closely related to *P. fibrillosum* Poepp. and probably belongs in *P.* subsect. *Canniphyllum.*

Other species of *P.* subsect. *Glossophyllum* described since the last revision by Krause are *P. acutifolium* K. Krause, *P. buntingianum* Croat, *P. liesneri* Croat, and *P. wurdackii* G. S. Bunting.

Though, as defined here, *P.* subsect. *Glossophyllum* ser. *Glossophyllum* consists only of species with more or less oblong blades, some of the species are somewhat anomalous. *Philodendron granulare* is much like other species in *P.* subsect. *Glossophyllum,* but it has a style that is unique in the group (Style Type E; see discussion of this under that species). *Philodendron brewsterense* and *P. ubigantupense* are still poorly known but appear to belong here. Perhaps the most doubtful is *P. dolichophyllum,* with 3–7 ovules, which is certainly high for this group; however, it is otherwise similar in most aspects to other members of the subsection. *Philodendron wendlandii,* placed by Krause in *P.* sect.

Baursia, seems to fit best in *P.* subsect. *Glossophyllum.* It differs from other members of subsection *Glossophyllum* in having a petiole that is usually broader than thick and sharply flattened adaxially and lacks an annular ring.

2. Philodendron ser. **Ovata** Croat, ser. nov. TYPE: *P. smithii* Engl.

Caudex longus vel brevis; internodia plerumque longiora quam lata; cataphylla plerumque decidua; petioli subaequantes laminam, teres vel subteres, cum annulo deficienti apice; lamina ovata vel ovato-triangulata, cordata vel sagittata ad basi; pistilla cum stylo plerumque "type B," rare C; ovaria 4–8-locularia; loculi uniovulati aut raro 2–5.

Philodendron ser. *Ovata* is a somewhat heterogeneous group characterized by blades ovate to ovate-triangular and cordate to subcordate at the base, with terete or subterete petioles lacking an annular ring at the apex. Locule number varies from 4 to 8, and each usually has a single ovule. Berry color is greenish white to white, yellowish to lavender for most species known, but *P. cotonense* and *P. wilburii* have orange fruits. Though only seven Central American species are known, the series undoubtedly has South American representatives.

The relationship with other members of *P.* subsect. *Glossophyllum* is uncertain. Aside from the usually solitary ovule per locule and usually somewhat spongy petiole, there is little resemblance between this group and typical members of *P.* subsect. *Glossophyllum,* which have elongated, rather than more or less ovate, blades. *Philodendron dominicalense* is the most doubtful member of the group; with the strongest possible similarity to *P. dodsonii* except for having a solitary ovule per locule (rather than about 20 ovules per locule as in *P. dodsonii*), it would appear that it might belong elsewhere. *Philodendron cotonense,* despite having 4–5 ovules per locule, appears also to belong to this section, considering its marked resemblance to *P. wilburii* and even *P. smithii.*

Central American species of *P.* ser. *Ovata* are: *P. cotonense, P. dominicalense, P. microstictum, P. smithii, P. straminicaule, P. sulcicaule,* and *P. wilburii.* With the exception of *P. smithii,* which ranges from Mexico to Nicaragua, *P.* ser. *Ovata* in Central America ranges from Nicaragua to Panama.

3. Philodendron subsect. **Oligocarpidium** (Engl.) Mayo, J. Linn. Soc., Bot. 100: 168. 1989. TYPE: *P. multispadiceum* Engl. (lectotype, designated by Mayo, 1990).

As defined by Krause, this was a group of four species that differed greatly from one another. *Philodendron deviatum* Schott has proven to be a synonym of *P. jacquinii* (which was placed by Krause in its own *P.* sect. *Macrogynium*). Another species that he included, *P. pittieri,* is just poorly preserved material of *P. hederaceum,* which Krause placed in his *P.* "Gruppe" *Solenosterigma* in *P.* sect. *Philodendron.* This leaves only *P. multispadiceum* Engl. and *P. muricatum* which, in my opinion, are quite unrelated. *Philodendron muricatum* is the oldest name for two other synonyms, *P. jenmanii* K. Krause and *P. scabrum,* which were placed by Krause in *P.* subsect. *Solenosterigma.* Though I am doubtful of the affinity between *P. hederaceum* and *P. muricatum,* it seems best to include *P. muricatum* in subsect. *Solenosterigma* because *P. muricatum* is clearly a member of *P.* sect. *Philodendron* and not *P.* sect. *Calostigma.*

This leaves only *P. multispadiceum,* which Mayo (1990) wisely chose as the type of *P.* subsect. *Oligocarpidium.* There are two Central American representatives of the subsection and a number of other undescribed South American species as well. The Central American species are *P. clewellii* and *P. heleniae.*

The subsection is distinguished by having a relatively large number of small (usually 4–10 cm long) inflorescences per axil. The plants are vines with long internodes and long-petiolate, narrowly ovate to ovate-cordate blades that have the basal veins either lacking or all free to the base and without the development of a posterior rib. Both Central American species represented have a type B style and an ovule sac surrounding the ovules.

4. Philodendron subsect. **Bulaoana** Mayo [as "*Bulaoanum*"], J. Linn. Soc., Bot. 100: 168. 1989. TYPE: *P. bulaoanum* Engl. (lectotype, designated by Mayo, 1989).

This subsection includes two species treated by Krause, *P. bulaoanum* and *P. acuminatissimum.* They probably represent the same species, a plant with deeply 3-lobed leaves and persistent, reddish brown cataphyll fibers. Currently the subsection is known only from South America. Krause treated this subsection as *P.* "Gruppe" *Doratophyllum,* but that name has no priority at the subsectional level (Mayo, 1990).

This subsection can be easily confused with and is perhaps inseparable from *P.* sect. *Tritomophyllum.* A moderately large number of South American species, including *P. barrosoanum* G. S. Bunting, *P. cataniapoense* G. S. Bunting (Bunting placed it in *P.* "Gruppe" *Doratophyllum*), *P. effusilobum*

Croat, *P. holtonianum* Schott, *P. hylaeae* G. S. Bunting (*P.* sect. *Calostigma*), *P. levelii* G. S. Bunting (similar to *P. barrosoanum*), *P. panduriforme* Schott, and *P. victoriae* G. S. Bunting might all belong here.

Philodendron subsect. *Bulaoana* and *P.* sect. *Tritomophyllum* are separated on weak features. Krause described his "Gruppe" *Doratophyllum* as having somewhat succulent petioles longer than the blade, a hastate blade, and ovaries that are several-ovulate near the base of the locule, whereas he described *P.* sect. *Tritomophyllum* as having tripartite blades with the lateral lobes erect or spreading, and the primary lateral veins more prominent than the minor veins. The ovary was described as 5–11-locular with the locules 1- or more-ovulate. The Central American species that appear to be closely related have one or two ovules per locule, whereas those of *P.* subsect. *Bulaoana* are described as having several ovules per locule. These distinctions are pretty weak, and further study of the members of both groups is necessary to decide whether the two groups should be merged.

5. Philodendron subsect. **Eucardium** (Engl.) Mayo, J. Linn. Soc., Bot. 100: 168. 1989. *Philodendron* "Gruppe" *Eucardium* Engl., Bot. Jahrb. Syst. 26: 535, 542. 1899. TYPE: *P. wallisii* Regel ex Engl.

This is a subsection of dubious status, based only on *P. wallisii*. The original description characterizes the subsection as having scarcely succulent petioles that are flattened to sulcate abaxially, cordiform blades, and 5–6-locular ovaries with a few sub-basal ovules per locule. Unfortunately, *P. wallisii* is a poorly known taxon for which, so far as is known, no material is extant.

Following his treatment of *Eucardium*, Krause discussed several poorly known species, all of which lacked inflorescences and for which no proper sectional placement was possible. Among these were *P. andreanum*, which is almost certainly related to *P. gigas*, a member of *P.* ser. *Velutina*. Listed among these dubious species are *P. latilobum* Schott and *P. obtusilobum* Miq. The former is a synonym of *P. panduriforme*, possibly a member of *P.* subsect. *Bulaoana*, which it most resembles. *Philodendron obtusilobum* is a poorly known species of unknown origin, known only from a single leaf. Its affinities remain unclear, but it appears similar to *P. lindenii* Schott or *P. rubens* Schott.

Also described among this group of unassigned species were *P. gloriosum* André and *P. mamei* André. These two species, along with *P. sodiroi* Hort., appear to be closely related and probably constitute a new section. *Philodendron pastazanum* K. Krause has similar features and probably belongs here as well. Another species known from the Amazonian lowlands of Peru and believed to be new is also in this group. All the species in this putative new section are terrestrial plants with a unique growth form for *Philodendron*. All have a short, repent, creeping stem with erect leaves clustered near the apex. The internodes are usually much broader than long and have cataphylls persistent, sometimes persisting somewhat intact. The petioles are frequently winged or undulate-winged along adaxial margins (but not *P. gloriosum*) and blades are typically quite attractive, sometimes mottled with paler green, sometimes (as in *P. gloriosum*) somewhat velvety. The group is restricted to South America chiefly in the upper Amazon region. Studies of the ovules are necessary to confirm these speculations, and investigations will be carried out as material becomes available.

5. Philodendron sect. **Tritomophyllum** (Schott) Engl., in Mart., Fl. bras. 3: 144. 1878. *Philodendron* grex *Tritomophyllum* Schott, Syn. Aroid. 107. 1856. *Baursia* sect. *Tritomophyllum* (Schott) T. Post & Kuntze, Lex. gen. phan. 63. 1903. TYPE: *P. tripartitum* (Jacq.) Schott (lectotype, designated by Mayo, 1990: 63).

The section is distinguished by having a scandent habit, three-lobed leaf blades and 1–2 ovules per locule. The section ranges from Mexico to South America, ranging as far as Ecuador on the Pacific slope and to Venezuela, the Guianas, and the Amazon basin. It is represented in Central America by six species: *P. angustilobum*, *P. anisotomum*, *P. cotobrusense*, *P. madronense*, *P. rothschuhianum* (Engl. & K. Krause) Croat & Grayum, and *P. tripartitum*. In South America there are a number of species with 3-lobed leaves, including: *P. barrosoanum*, *P. cataniapoense*, *P. effusilobum*, *P. holtonianum*, *P. hylaeae*, *P. levelii*, *P. panduriforme*, and *P. victoriae*, all now tentatively placed in *P.* subsect. *Bulaoana*, which might belong in *P.* sect. *Tritomophyllum*. Certainly *P. hylaeae*, with 1–2 ovules per locule and a strong similarity with *P. tripartitum*, would appear to be closely related to *P.* sect. *Tritomophyllum*.

Bunting (1986) placed *P. cataniapoense* in *P.* sect. *Oligospermium* "Gruppe" *Doratophyllum* (now *P.* subsect. *Bulaoana*) but this species has a single ovule per locule, elongate internodes, and deciduous cataphylls. It may properly belong with *P.* sect. *Tritomophyllum*.

Some of the above-mentioned South American species are doubtfully included here, since they

have several (more than 1 or 2) ovules per locule. *Philodendron levelii* has 2–4 sub-basal ovules, and *P. barrosoanum* has 4–6 ovules attached above the base. *Philodendron victoriae* is apparently closely related to *P. barrosoanum* so it probably has similar ovules. It is possible that none of these species belong to *P.* sect. *Tritomophyllum*, but on the other hand they do not closely match *P. bulaoanum*, the type of *P.* subsect. *Bulaoana*, either.

6. Philodendron sect. **Schizophyllum** (Schott) Engl., in Mart., Fl. bras. 3: 144. 1878. *Philodendron* grex *Schizophyllum* Schott, Syn. Aroid. 104. 1856. TYPE: *P. pedatum* (Hook.) Kunth (lectotype, designated by Mayo, 1990: 63).

The section is a small but natural group of 6–7 scandent species with irregularly pedatisect leaves, 3–4 ovules per locule, and sometimes scaly petioles, primarily restricted to eastern South America and the Amazon basin, but with one species, *P. pedatum*, more widespread and ranging to northwestern Colombia. The species may occur in Central America, according to horticulturist John Hall of Costa Rica, who illustrated such a plant supposedly from the Osa Peninsula. Characteristically, no material was collected and this claim cannot be refuted.

7. Philodendron sect. **Polytomium** (Schott) Engl., in Mart., Fl. bras. 3: 145. 1878. *Philodendron* grex *Polytomium* Schott, Syn. Aroid. 108. 1856. TYPE: *P. radiatum* Schott (lectotype, designated by Mayo, 1990: 63).

The section is a small group of 7–8 species with pinnately or bipinnately lobed leaves from the West Indies, Central America, and northern South America. Plants are vines or appressed climbers with more or less terete petioles, generally deeply lobed, large, moderately coriaceous blades, and flowers with several axillary or sub-basal ovules per locule. Only one species, *P. distantilobum* K. Krause, was reported for the Amazon basin, but another species, *P. pinnatifidum*, placed erroneously, I believe, in *P.* sect. *Macrogynium*, really belongs here as well. It is also a species occurring in the upper Amazon basin. Two additional species, *P. angustisectum* Engl. and *P. elegans* K. Krause, occur in Colombia. *Philodendron fendleri* occurs in Trinidad and northern Venezuela, and *P. lacerum* (Jacq.) Schott occurs in the Greater Antilles (Cuba, Jamaica, and Hispaniola). One poorly known species, *P. houlettianum* Engl., has been reported from French Guiana but no material exists to confirm what it is. The most widespread species in the section, *P. radiatum*, occurs in Central America, ranging from Mexico (San Luis Potosí) to Colombia (Antioquia). *Philodendron radiatum* var. *pseudoradiatum* is endemic to the State of Chiapas in Mexico. Central American species in *P.* sect. *Polytomium* are *P. warszewiczii*, ranging from Mexico to Nicaragua, and *P. dressleri*, which is endemic to Mexico.

Mayo (1986), following a cladistic survey of inflorescence types, concluded that *P. fendleri* belonged in a group with *P. melinonii* and *P. pedatum*. Based on overall morphology I would conclude that the three species are not closely related. The latter is, in my opinion, a member of a distinctive section, *P.* sect. *Schizophyllum*. *Philodendron melinonii* Brongn., a distinctive species with cordate blades and placed by Krause in *P.* sect. *Macrolonchium*, is in my opinion, not related to either of the sections with lobed leaves.

8. Philodendron sect. **Macrogynium** Engl., Bot. Jahrb. Syst. 26: 553. 1899. TYPE: *P. hoffmannii* Schott.

Philodendron sect. *Macrogynium* is one of two small sections treated by Krause (1913) (the other being *P.* sect. *Camptogynium*). *Philodendron* sect. *Macrogynium* consists of a single species, *P. jacquinii* (treated by Krause as *P. hoffmannii*). Both sections are represented by scandent species, distinguished by having the style prolonged and much narrower than the ovary and a single ovule per locule. Despite these similarities the two sections are very different from one another. *Philodendron jacquinii* (*P.* sect. *Macrogynium*) has setose stems and thin, veiny, ovate-cordate blades which may be deciduous during the dry season. Its spathe is bulbous and roomy inside, quite unlike most species. The style, though narrowed to the apex, has a typical, hemispheroid stigma. For differences with *P.* sect. *Camptogynium*, see below.

Philodendron brevispathum, with its similarity to *P. jacquinii*, might be considered a relative, but the former has branched scales, not simple trichomes on stems and petioles; a normal, sessile style; and 6–14 ovules per locule with axile placentation, rather than 2 ovules per locule and sub-basal placentation for *P. jacquinii*.

This section appears, at least on the surface, to be natural. No other species known is alike either morphologically or ecologically. Its thin, veiny leaves are deciduous in the dry season and the large colorful infructescences are prominently displayed in a mostly deciduous environment.

9. Philodendron sect. **Camptogynium** K. Krause in Engl., Das Pflanzenreich IV. 23Db (Heft 60): 3, 127. 1913. TYPE: *P. longistilum* K. Krause

In contrast to *P. jacquinii*, which has setose stems and thin cordate blades with prominent veins, *P. longistilum* (*P.* sect. *Camptogynium*) has glabrous stems and oblanceolate, subcoriaceous blades with obscure primary lateral veins. The chief reason for its status as the only member of a section is the peculiar prolonged style, which is deflected to one side and has a cupular apex. It is perhaps not as unique as Krause assumed. Other species are now known to have prolonged styles deflected to one side, among them two undescribed species with cordate blades from western Ecuador, one based on *Camp 3701* and the other on *Jaramillo et al. 25449*. However, neither has a cupular style apex. These perhaps represent another section, or more likely Krause's *P.* sect. *Camptogynium* may have to be incorporated in *P.* sect. *Calostigma*, where it might be easily accommodated.

KEY TO THE SECTIONS AND SUBSECTIONS OF *P.* SUBG. *PHILODENDRON*

1a. Pistils usually 2-locular, rarely 3-locular; eastern South America and Amazon basin ..... *P.* sect. *Philopsammos*
1b. Pistils 4–10-locular; throughout the range of the genus.
2a. Plants with primary lateral leaf veins moderately obscure; all South American (excludes *P. wendlandii*, which is transferred to *P.* sect. *Calostigma*) ..... *P.* sect. *Baursia*
2b. Plants with primary lateral leaf veins usually much more prominent than the minor veins.
3a. Pistil with style much narrowed and much prolonged beyond the body of the ovary and much narrower than ovary.
4a. Style turned toward apex, perpendicular to the body of the ovary; South American species only ..... *P.* sect. *Camptogynium*
4b. Style straight, directed in the same axis as the ovary; Central and South America ..... *P.* sect. *Macrogynium* (*P. jacquinii*)
3b. Pistil with style about as broad as the ovary, scarcely prolonged beyond body of ovary.
5a. Blades 3-lobed or deeply incised-lobate.
6a. Blades 3-lobed; ovules 1–3 per locule, basal or sub-basal. [Note: *P.* subsect. *Doratophyllum* with 3-lobed blades would also key here. See the discussion after that subsection.] ..... *P.* sect. *Tritomophyllum* [*P. angustilobum* (perhaps this belongs in *P.* subsect. *Macrobelium* (Schott) Engl.), *P. anisotomum*, *P. cotobrusense*, *P. madronense*, *P. rothschuhianum*, *P. tripartitum*]
6b. Blades incised-lobate; ovules 2–8 per locule, sub-basal or axile.
7a. Blades divided along the anterior lobe into two or more divisions, each division in turn terminating with much smaller lobes; petioles sometimes with trichome-like scales; South America only ..... *P.* sect. *Schizophyllum*
7b. Blades pinnately or bipinnately lobed, the divisions ± uniform along the anterior lobe; petiole never scaly; Central and South American species ..... *P.* sect. *Polytomium* [*P. dressleri*, *P. radiatum*, *P. warszewiczii*]
5b. Blades entire, sometimes with the anterior lobes markedly concave, but the blade not markedly 3-lobed or incised-lobate.
8a. Pistils with axile placentation; ovules usually 15 or more per locule, seldom with as few as 10 per locule, rarely fewer ..... *P.* sect. *Philodendron*
9a. Blades cordate to subcordate or sagittate at base; petioles various.
10a. Petioles ± D-shaped in cross section, sharply flattened adaxially, sometimes also with the lateral margins raised.
11a. Stems with internodes much broader than long ..... *P.* subsect. *Macrolonchium* (Schott) Engl. [*P. fragrantissimum*]
11b. Stems with internodes about as broad as long or longer than broad ..... *P.* subsect. *Platypodium* (Schott) Engl. [*P. brunneicaule*, *P. copense*, *P. findens*, *P. fortunense*, *P. pterotum*]
10b. Petioles terete or subterete.
12a. Petioles warty at apex; South American species (excluding *P. grandipes* erroneously placed here by Krause); *P. ornatum* Schott and relatives ..... *P.* subsect. *Psoropodium* (Schott) Engl.
12b. Petioles smooth or conspicuously scaly but not merely warty at apex.
13a. Plants scandent; internodes much longer than broad; cataphylls usually deciduous; blades cordate ..... *P.* subsect. *Solenosterigma* (Klotzsch ex Schott) Engl. [*P. brevispathum*, *P. purpureoviride*, *P. hederaceum*]
13b. Plants usually not scandent, either terrestrial or appressed-climbing with internodes broader than long or not much longer than broad; cataphylls usually persistent, rarely deciduous; blades ovate to sagittate.
14a. Plants with petioles scaly ..... *P.* subsect. *Achyropodium* (Schott) Engl. [*P. glanduliferum*, *P. hammelii*, *P. malesevichiae*, *P. squamipetiolatum*, *P. squamicaule*, *P. verrucosum*]
14b. Plants with petioles smooth, not scaly ..... *P.* subsect. *Philodendron*
15a. Cataphylls deciduous intact or sometimes becoming fibrous but soon deciduous ..... *P.* ser. *Philodendron* Schott [*P. giganteum* (not in Central America)]
15b. Cataphylls persisting as a mass of fibers.

16a. Blades matte on lower surface.
17a. Blades matte, not velvety on upper surface, whitish and glaucous on lower surface ..... *P.* ser. *Impolita* Croat [*P. hebetatum, P. strictum, P. thalassicum*
17b. Blades velvety on upper surface, not whitish and glaucous on lower surface ..... *P.* ser. *Velutina* Croat [*P. gigas*]
16b. Blades usually semiglossy, never whitish or glaucous, on lower surface.
18a. Sap brown to clear, never chalky ..... *P.* ser. *Fibrosa* Croat [*P. alticola, P. antonioanum, P. breedlovei, P. chiriquense, P. dodsonii, P. grandipes, P. jodavisianum, P. lazorii, P. llanense, P. panamense, P. pirrense, P. purulhense, P. scalarinerve, P. schottianum, P. tenue*]
18b. Sap white and chalky ..... *P.* ser. *Albisuccosa* Croat [*P. albisuccus*]

9b. Blades acute to obtuse at base; petioles subterete and smooth ..... *P.* subsect. *Canniphyllum* (Schott) Mayo [*P. chirripoense, P. cretosum, P. roseospathum*]

8b. Pistils with basal or sub-basal placentation; ovules few per locule, usually fewer than 5, seldom up to 8, rarely as many as 12 (but with some locules in the same inflorescence with as few as 6 ovules per locule) ..... *P.* sect. *Calostigma*
19a. Plants usually appressed hemiepiphytic climbers; internodes frequently as long as wide or longer than wide; widespread in both Central and South America.
20a. Blades deeply 3-lobed; cataphylls persisting in a dense, reddish brown layer of fibers; South American species only; *P. acuminatissimum* Engl., *P. bulaoanum* Engl ..... *P.* subsect. *Bulaoana* Mayo
20b. Blades not at all 3-lobed, cordate, sagittate, or ± oblong; cataphylls deciduous or persistent, fibrous or intact; widespread in both Central and South America.
21a. Inflorescences both small and numerous, usually more than 6 per axil, less than 5 cm long ..... *P.* subsect. *Oligocarpidium* (Engl.) Mayo [*P. clewellii, P. heleniae*]
21b. Inflorescences of normal size, typically 1–few and more than 5 cm long.
22a. Pistils with several ovules per locule; petioles rarely with purple ring at apex; blades sagittate or cordate at base ..... *P.* subsect. *Macrobelium*
23a. Cataphylls deciduous.
24a. Leaf blades with minor veins not at all etched into upper surface ..... *P.* ser. *Macrobelium* (Schott) Croat [*P. advena, P. annulatum, P. aromaticum, P. coloradense, P. dwyeri, P. edenudatum, P. ferrugineum, P. grayumii, P. knappiae, P. mexicanum, P. platypetiolatum, P. sagitti-folium, P. sousae, P. subincisum, P. verapazense, P. zhuanum*]
24b. Leaf blades with minor veins etched into upper surface ..... *P.* ser. *Ecordata* Croat [*P. brenesii, P. crassispathum, P. davidsonii, P. lentii, P. niqueanum*]
23b. Cataphylls persistent.
25a. Cataphylls weathering and persisting as fibers ..... *P.* ser. *Reticulata* Croat [*P. jefense, P. tysonii*]
25b. Cataphylls persisting intact; stems markedly succulent ..... *P.* ser. *Pachycaulia* Croat [*P. basii*]
22b. Pistils with ovules solitary (or sometimes 2, as in *P. wilburii*) in each locule; petioles frequently with purple ring at apex (*P.* subsect. *Glossophyllum*); blades elongate (*P.* ser. *Glossophyllum*) or ± ovate (*P.* subsect. *Glossophyllum* ser. *Ovata*).
26a. Blades mostly ± oblong and acute to narrowly subcordate at base; petioles frequently with a purple ring at apex ..... *P.* subsect. *Glossophyllum*(Schott) Engl.; *P.* ser. *Glossophyllum* (Schott) Croat [*P. auriculatum, P. bakeri, P. brewsterense, P. correae, P. dolichophyllum, P. folsomii, P. granulare, P. immixtum, P. ligulatum, P. morii, P. pseudauriculatum, P. ubigantupense, P. utleyanum, P. wendlandii*]
26b. Blades ovate to ovate-triangular, cordate to subcordate at base; petioles usually lacking a purple ring at apex ..... P. subsect. Glossophyllum; *P.* ser. *Ovata* Croat [*P. cotonense, P. dominicalense, P. microstictum, P. smithii, P. straminicaule, P. sulcicaule, P. wilburii*]
19b. Plant habit unknown; internodes much broader than long; Colombia (exact locality unknown) ..... *P.* subsect. *Eucardium* (Engl.) Mayo

Note: For an outline of the sectional classification of *Philodendron* subg. *Philodendron* in Central America see Appendix 3.

Morphology of Vegetative Structures

Anatomy

Vegetative anatomy. (Section on Vegetative Anatomy contributed by R. C. Keating; vouchers will be cited by Keating (in press)).

General comments. *Philodendron* has secretory ducts present in all morphological parts. These occur mostly as 2–4 "files" in vascular bundles. Laticifers are of the non-anastomosing type, simple and articulated (French, 1988). The genus also has secretory ducts present in roots, stems, leaves, and inflorescences. The roots have a sclerotic hypodermis.

Leaf surfaces. Cuticle smooth or occasionally rough on both surfaces. *Epidermis*: adaxial cells polygonal (1–2:1), straight-sided. Abaxial cells similar to or larger than adaxial cells or more elongate (2–4:1 l/w). *Stomata*: abaxial, randomly oriented, brachyparacytic to brachyparahexacytic. *Venation*: secondary veins parallel with reticulate higher order veins.

Leaf Cross Section. Cuticle of medium thickness, may intrude deeply along anticlinal walls of epidermal cells. Abaxial cuticle may be thinner and smooth or striate. *Epidermal cells*: large or small, square to columnar or tile-like adaxial cells, larger abaxially, or same size; outer and inner walls flat. *Stomata* level with surface with conspicuous double cuticular flanges often present. *Hypodermis*: absent or as 1–3 layers present on adaxial side of midrib, or as isodiametric cells beneath both epidermal layers (in *P. crassispathum*, hypoderm of 1–4 layers adaxially and 2–3 layers abaxially), cells may contain dark material. *Mesophyll*: palisade 1–4 layers of elongated or rounded cells, usually packed with plastids; occupying 10–30% of lamina. Spongy layers up to 15 cells deep. *Air spaces*: large, substomatal cylinders perpendicular to surface; 30–90% space in spongy layer; or air cavities irregular in some species. Paradermally, spongy tissue with one layer of unarmed cells over abaxial epidermis, then small cells or short-armed cells surrounding large air cavities extending from stomata to palisade cells; 3–5 spongy cells per uniseriate partition. Large cavities in midrib separated by uniseriate partitions of ground tissue, partitions 3–4 cells long between junctions. *Collenchyma*: 4–5 discrete subepidermal layers of small cells on abaxial side of midrib, often extending to vascular bundles.

Vascular bundles. One to several large bundles in the midrib, often at corners of a net-like aerenchyma; well delimited, with 1–5 large metaxylem cells, next to a small, round or elliptic phloem strand. *Sclerenchyma*: fibers, usually as a phloem cap 1–3 layers deep, and less commonly as a xylem cap. Some laminar bundles ensheathed with fibers. Fibers having up to 5 discrete wall layers. Xylem cells often ringed with a single layer of small parenchyma cells. *Secretory ducts*: occasional in midlamina or midrib with 1–2 layers of epithelium. *Laticifers*: lateral to vascular bundles, 2–3 per bundle, outside fibers, often with short processes protruding between adjacent mesophyll cells; containing dark amorphous contents. *Starch*: abundant in midrib ground tissue, not seen in lamina. *Crystals*: raphides common or uncommon in single packets in short or elongate cells, ends protruding across partitions into both adjacent air spaces, or in large rounded cells of upper or lower mesophyll. Raphide packets occasionally surrounded by dark sheaths within the cell (in *P. crassispathum* crystal cells elongated parallel with vascular bundles). Druses rare or common, often coarse and sharp-pointed, in rounded cells in palisade and spongy tissue partitions. Crystal sand absent or common in most mesophyll cells.

Petiole Cross Section. Cuticle smooth and thin. Epidermis of small cells, level or rounded on surface and inner walls rounded to angular. Hypodermis of 2–4 layers. Collenchyma beneath hypodermis as a continuous band of 4–8 layers of angularly thickened, longitudinally elongated cells (8–10:1). *Chlorenchyma*: up to 5 rows of cells inside collenchyma, and in addition, in *P. jodavisianum*, as perpendicular partitions dividing the collenchyma band, and reaching subepidermal layers. Ground tissue of various sizes of parenchyma cells among numerous small to medium-sized air cavities separated by uniseriate partitions of up to 3 cells long. Cells often longitudinally elongated (3–6:1 l/w). Vascular bundles numerous and scattered, mostly oriented with phloem facing perimeter. Bundles are parallel in longitudinal section with some higher order angular connections. Xylem of 1–3 protoxylem cells per bundle, with spiral to annular thickenings, and occasionally one metaxylem element. Phloem of sieve cells and companion cells forming organized grid. In longitudinal section, sieve elements with horizontal to 45° oblique end walls. *Sclerenchyma*: fibers forming phloem cap, 2–4 cells deep, usually not fully surrounding phloem laterally. In some species, fiber caps surrounding xylem and phloem or ensheathing entire bundle.

Secretory ducts surrounded by epithelium and 1–2 rows of additional small cells, very common in

collenchyma and common in ground tissue. *Laticifers*: 1–3, found laterally on one or both flanks of vascular bundles; non-articulated. Starch common throughout ground tissue, rare in collenchyma. *Crystals*: narrow raphide cells occasional, oriented across aerenchyma partitions with ends pointing into air cavities, or cells randomly oriented. Druses present subepidermally and in cells bordering air cavities. Small groups of small prismatics common in ground tissue.

Stem Cross Section. 1–3 cm diam. Cuticle of medium thickness, smooth to rough-surfaced. Epidermis of very small cells, outer walls rounded. *Cork*: cells may be present subepidermally. *Hypodermis*: a subepidermal layer of large cells, over 1–2 layers of thick-walled fibers, followed by thin-walled periderm cells. *Collenchyma*: angularly-thickened cells, 3–10 layers deep, beneath periderm. Cortical ground tissue of loosely packed parenchyma. *Air cavities*: cell-sized or smaller in all ground tissue. *Central cylinder*: weakly delimited by a circle of vascular bundles, some of which tangentially fused in pairs or threes by phloem fibers and confluent phloem strands. Cortical bundles randomly scattered. Vascular bundles collateral and highly variable in form and orientation. Compound bundles numerous in central cylinder with irregular fiber strands in center of groups of 2–6 bundles. Small phloem strands outside fibers facing groups of 1–2 metaxylem elements on outer side. Simple collateral bundles may have a large wide strand of fibers surrounding phloem, a very small irregularly shaped strand of fibers, or no fibers. Fibers having up to 7 discrete wall layers visible.

Secretory ducts small and numerous in collenchyma and outer cortex, less common elsewhere. Duct cavities surrounded by two modified layers of small cells; contents of cavities testing positively for lipids. *Laticifers*: absent or present as 1–3 cells lateral to many vascular bundles, occasional in phloem. *Crystals*: raphides as single packets in elongate cells, most common in central cylinder. Druses of all sizes common in small cells in cortex.

Vascular anatomy. The configuration of shoot vasculature of *Philodendron* has been extensively studied by French and Tomlinson (1980, 1981, 1984). They reported the genus to be one of the most diverse in the family from an anatomical point of view. The axis of the vascular system of *Philodendron* is continuous throughout the stem because the renewal shoots develop precociously and because the morphologically terminal parts of the stem soon become branches (French & Tomlinson, 1984). All species of *Philodendron* examined by French and Tomlinson have an "independent cortical vascular system of traces that pass from the leaf into the cortex, but without entering the central cylinder." Generally the cortex is wide with 3–5 or more indistinct series of bundles. Cortical bundles are collateral, typically with a fibrous sheath next to the phloem. Major leaf traces enter the cortex at an acute angle and promptly enter the central cylinder, while smaller traces enter the cortex at a less acute angle and may enter the central cylinder well below where they entered the cortex. No endodermis was observed by French and Tomlinson for any of the species.

Philodendron subg. *Philodendron* has secretory resin canals occurring in the cortex. These consist of a schizogenous space lined with 2–3 layers of epithelial cells and contain a Sudan IV-staining resin (French & Tomlinson, 1984). The central cylinder is separated from the cortex by an arrangement of vascular bundles into which the leaf traces merge. Bud traces are equal on both sides and form an arc near the periphery of the central cylinder before joining with the axial bundles.

In their survey of 3-dimensional arrangement of vascular bundles, leaf traces and axial bundles were distinct, with the leaf traces consistently collateral with protoxylem and usually with a prominent sheath of sclerenchyma next to the phloem. The axial bundles were divided roughly into five groups, four of which pertain to *P.* subg. *Philodendron.*

In the *P. hederaceum* pattern (French & Tomlinson pattern 1) there are simple collateral bundles with some bipolar bundles in the central cylinder of the internodes with thin-walled and non-lignified ground tissue.

Another relatively rare pattern involving *P.* sect. *Baursia* (but not a Central American representative of the section) and *P. jacquinii* (pattern 3 of French & Tomlinson) has compound bundles throughout the central cylinder with individual compound bundles consisting of strands of xylem and phloem separated from each other by sclerenchyma "in the form of a partial or complete sheath" (French & Tomlinson, 1984). In *P. jacquinii* leaf traces enter the central cylinder but make a variety of configurations, sometimes including pairing before joining the compound bundles. Compound bundles do not make a particularly straight course, sometimes bundling and pairing within and between compound bundles.

A pattern of vascular bundle traces exhibited by *P. fragrantissimum* and *P. roseospathum* (French & Tomlinson pattern 4) is similar to pattern 3 except that "the pattern of the vascular components with

compound bundles is less clear because components are not separated by sclerenchyma" (French & Tomlinson, 1984). The sclerenchyma occupies the central core but does not isolate individual bundle components.

The pattern for *P. mexicanum* and *P. sagittifolium* (French & Tomlinson pattern 5), described as the most common in the genus, has axial bundles strictly amphivasal with a central core of phloem and a peripheral region of xylem. The tracheary elements may form a more or less continuous cylinder or may be arranged in clusters around the phloem. Leaf traces penetrate the central bundle and fuse with the central cylinder, while the sclerenchyma sheath of the trace migrates to the center of the axial bundle.

Habit and growth patterns. In terms of growth habit *Philodendron* is clearly one of the most variable genera in the Araceae (Blanc, 1977a, 1977b, 1978, 1980; French & Tomlinson, 1981). The habit ranges from terrestrial to epiphytic or hemiepiphytic (primary or secondary). Secondary hemiepiphytes may be vines or appressed-climbers.

Relatively few *Philodendron* species are terrestrial, although a few are consistently terrestrial. These include *P. glanduliferum, P. grandipes, P. malesevichiae,* and perhaps *P. hammelii* (known only from a single collection). The stem of *P. glanduliferum* (Fig. 198) is usually repent. Other species are mostly terrestrial, but sometimes hemiepiphytic: e.g., *P. basii, P. roseospathum* var. *roseospathum,* and *P. warszewiczii. Philodendron knappiae* is about equally terrestrial or hemiepiphytic. Label data regarding habit on herbarium collections are often suspect, with many herbarium labels using the term "epiphyte" when in fact the collections were probably rooted in the soil and were therefore technically hemiepiphytic. In addition, although many species have collections reporting them to be terrestrial, the majority were probably found on the ground as a result of accidentally falling from trees. Many collections are naturally made in virgin forest areas where man-made disturbances such as road building give access to the forest. In such areas, and especially in the regrowth along road cuts, aroids are very common. Many *Philodendron* species, e.g., *P. lentii* (Fig. 261) and *P. squamicaule* (Fig. 382), persist in excellent condition on steep roadbanks because the steep clay slopes allow adequate drainage for the plants to survive. Still, these are somewhat unusual situations. On the other hand, stream banks often provide similar habitats.

Many members of *P.* subg. *Philodendron* are hemiepiphytic, meaning that they are growing on trees as appressed climbers or as vines, while being rooted in the soil. There are two types of hemiepiphytes (Putz & Holbrook, 1986). Primary hemiepiphytes begin their lives when seeds germinate on the host tree, in the same way as true epiphytes, then go on to develop slowly until they reach sufficient age and size to begin developing long aerial roots that may eventually reach the ground. This growth strategy enables the species to quickly attain a height where light is adequate but nutrients are more difficult to obtain. Not surprisingly, one of the most successful species with this life form is *P. megalophyllum* Schott, which often lives on ant nests from which it obtains extra nutrients. No Central American species are known to live exclusively with associated ants, although occasional ant nests occur among the cluster of roots of many species. The roots hold the otherwise fragile ant nest to prevent it from being washed away in the rain. Examples of this type of hemiepiphyte are *P. goeldii* G. Barroso, *P. solimoesense* A. C. Sm., *P. megalophyllum* (all from South America), and *P. radiatum* (Fig. 1), the only species known with this growth form in Central America.

Secondary hemiepiphytes (Putz & Holbrook, 1986) start their lives on the ground or on tree trunks near the ground (where they may send roots to the ground) and climb trees where they become adults and may lose their connection with the ground. Most *Philodendron* sect. *Philodendron* are members of this group.

As is the case with most Araceae, adult plants of *P.* subg. *Philodendron* have homeophyllous monopodial growth[11] (monophyllous sympodial of Ritterbusch, 1971) with each article bearing a cataphyll and a leaf. When the plant is mature, each article is terminated by an inflorescence (Ray, 1986, 1987b) or its aborted remains (Engler, 1877; Ritterbusch, 1971). The branching pattern for *P.* subg. *Philodendron* has the prophyll following each internode suppressed, with a single foliage leaf followed by the inflorescences and with the internode subtending the prophyll of the elongation shoot being suppressed. Growth patterns for *P.* subg. *Philodendron* were diagrammed schematically by Engler

[11] "In monopodial growth, flowering occurs on axillary short shoots and does not interrupt the formation of the main shoot by a single apex. In monophyllous sympodial growth, after the shoot terminates in an inflorescence (which often aborts at the primordial stage), each continuation shoot will produce only a single foliage leaf before terminating in another inflorescence, and being replaced by another continuation shoot with one foliage leaf" (Ray, 1987b).

(1877) and Ray (1988) and discussed in detail by French and Tomlinson (1981). In contrast to adult plants of *P.* subg. *Philodendron*, the juvenile growth phase (with a few exceptions) has monopodial (actually anisophyllous sympodial) growth with an article bearing an indeterminate number of foliage leaves before terminating in the first (likely aborted) inflorescence, marking the transition into homeophyllous sympodial growth where each article has a fixed number of leaves and is terminated by an inflorescence or its aborted remains. This transition does not mean that stem has reached maturity. It has only made a transition from monopodial (actually anisophyllous sympodial) growth to homeophyllous sympodial growth. At this point, the plant is probably still not mature, and while every article will end in an infloresence, these will all be aborted. Later, after further thickening of the stem, the shoot will become mature, and this will be indicated by the fact that the inflorescences do not always abort (T. Ray, pers. comm.).

In contrast to *P.* subg. *Philodendron*, *P.* subg. *Pteromischum* has monopodial growth only up until the time of flowering when it is followed by anisophyllous sympodial growth, wherein the stem articles bear a variable number of leaves before producing another inflorescence. Each new branch forms from a bud in the "axil of the penultimate leaf of the previous unit" (French & Tomlinson, 1981). Both *P.* subg. *Pteromischum* and *P.* subg. *Philodendron* have development of the stem beyond each terminal inflorescence. Thus although *P.* subg. *Philodendron* appears to have an unbranched stem with an inflorescence in each leaf axil it is really producing a new branch after producing each leaf. Close examination will show that a bud for the renewal shoot occurs on each article just below the point of overlap of the sheath edges of the cataphyll (prophyll of Ray, 1987a). It is from this point that the new branch will form. There is also a second, supernumerary bud which lies below (proximal to) the bud for the renewal shoot. This acts as a reserve meristem, lying dormant unless the stem is severed just distally to it (French & Tomlinson, 1984).

Unlike *P.* subg. *Philodendron*, *P.* subg. *Pteromischum* typically does not branch after the production of each new leaf and therefore lacks comparable branch buds. The inflorescences are never produced terminally on determinate lateral branches (Grayum, 1996).

Internode length and width are altered markedly as the plant climbs, with the internodes getting ever shorter and thicker. Ray (1986) has shown a direct correlation between the length and width of an article (one segment of the stem) demonstrating that the length-width ratio is fixed and varies according to a set pattern. Ray (1987b) categorized four different types of stem segments based on where the leaf was attached to the stem. In *P.* subg. *Philodendron* all species had the petiole attached to the lower end of the stem segments, and these are referred to as "hypophyllous segments." Most species of *P.* subg. *Pteromischum* have "hyperphyllous segments" where the petiole is attached to the upper end of the stem segment. "Ambiphyllous segments," where the stem segment is so short that the petiole is attached across the entire segment, is also known in *P.* subg. *Pteromischum* and is also the most common type elsewhere in the family. The fourth type of sympodial stem segment, referred to as "peraphyllous segments" and presently known in the family only in *P.* subg. *Pteromischum*, has the stem segments elongated and extended below the point of attachment of the cataphyll.

Most members of *P.* subg. *Philodendron* have leaves that turn from juvenile to adult gradually as the plant climbs so that there is no abrupt transition to adult foliage.

Although not as pronounced as in *Monstera* or *Syngonium*, leaf dimorphy is present in some species of *Philodendron*. For example, in *P. hederaceum* var. *hederaceum* juvenile leaves have short petioles tightly appressed to the tree, more or less like the "shingle" leaves of *Monstera*. They are also dark blackish green and velvety above and often somewhat purplish violet beneath. The adult plants have spreading leaves with longer petioles and smooth, semiglossy blades. The velvety blades seem to be associated only with the earliest growth. Once the plant grows up high enough on the tree the leaves become smooth and semiglossy. Further growth, even when it represents a reversion to smaller-leaved forms, results in the same smooth, semiglossy texture as that of the adult.

Philodendron hederaceum and other scandent species tend to climb high up the trunk of the tree then spread into the canopy and finally often hang down from branches before they flower. *Philodendron jacquinii* often has a similar habit. Some scandent species, such as *P. brevispathum* and *P. sulcicaule*, typically sprawl over lower vegetation rather than high in the canopy.

The amount of internode elongation varies immensely in some vining species, such as *P. immixtum*, *P. hederaceum*, and *P. sulcicaule*, with internodes 10–20 cm long (even longer on plants that are juvenile or have reverted to a "searching mode" as the result of dislodgement from the tree). Usually internode length varies considerably depending on the light and nutrients available for growth. Even

fully adult plants with very short internodes can be induced to produce longer internodes in cases where the plant is accidentally displaced from its growing situation or if it becomes heavily shaded.

Some species have evolved the ability to produce flagellate branches in an attempt to reposition themselves. These have long slender internodes and reduced leaves. At first the flagelliform growth spreads laterally, but if no other growth support is in the immediate vicinity the branch inclines toward the ground where it may creep across the surface and ascend another tree. Blanc (1980) referred to these as "flagelles" or "stolons." Ray (1987b) indicated that these flagellate branches are usually developed when a plant overgrows its support or is accidentally dislodged, but in some species, e.g., *P. fragrantissimum*, the flagellate branches may develop from a normally growing plant (Croat, 1978). *Philodendron linnaei* Kunth, a South American species, has developed this method of locomotion to an extreme. That species produces a series of rosulate clusters of leaves all interconnected by more slender flagellate stems, which ascend the tree trunk. After a period of rapid growth resulting in long, narrow internodes with the leaves reduced to small scales, the plant produces a series of short thick internodes, each of which is associated with an increasingly larger leaf, and leaves arranged in a tight rosette (Ray, 1987b). Ray (pers. comm.) reports that "with only a few exceptions, flagellar shoots do not occur in species with homeophyllous growth. Flagellar shoots are almost universal among climbing species with anisophyllous or intermittent homeophyllous growth, but almost totally lacking among climbing species with homeophyllous growth."

Stems. Stems vary considerably in length depending on the nature of growth. Vines, such as *P. hederaceum*, may produce stems well over 30 m long, whereas the more slow-growing appressed climbing hemiepiphytes rarely have stems more than about 2 m long. The youngest part of the stem bears most of the leaves and has the newest root growth including the most active feeder roots. Older portions of the stem have thick, strong roots usually tightly fastened to the tree, anchoring it in place. Some roots all along the stem extend downward along the stem and may lead all the way to the ground. The older portion of the stem is often devoid of any leaves and usually lacks even cataphyll fibers. The bare stem clearly shows the petiolar and cataphyll scars (Figs. 9–12). See discussion below. Inspection usually shows that the older portions of the stem have been at some time attacked by root borers so there may be surface damage or more likely active root borers in the center of the stem. Eventually the lower part of the stem rots away as the stem climbs higher on the side of the tree.

Stems of *Philodendron* are typically unbranched, but may be branched naturally, as in many species of *P.* subg. *Pteromischum*, or through injury. Commonly internodes become increasingly shorter and thicker toward the apex of the stem on appressed-climbing plants, but some species, e.g., *P. fragrantissimum*, may from time to time begin to produce long slender internodes to enable the plant to enter a colonizing mode (see above section on "Habit and Growth Patterns").

Mayo (1991) described differences in the branching pattern of *P.* subg. *Philodendron* and *P.* subg. *Meconostigma*. While most *P.* subg. *Meconostigma* have very short internodes, some species, e.g., *P. leal-costae* Mayo & Barroso and *P. corcovadense* Kunth, have elongated internodes. In these species the elongated internode of each article is the one between the cataphyll (prophyll of Ray, 1987a) and the succeeding foliage leaf, while the internode preceding the cataphyll is abbreviated. In *P.* subg. *Philodendron* the elongated internode is the hypopodial internode (which precedes the cataphyll), while the internode between the cataphyll and the foliage leaf is the abbreviated one.

Stems of *Philodendron* are typically rich in taxonomic characters, and together with their associated cataphylls, yield some of the best key characters for identification. Normally these stem characteristics are useful only at the specific level, but Grayum (1996) has found the dried stem color to be useful in separating the two sections of *P.* subg. *Pteromischum*. Unlike most *Anthurium* species, which have internodes so short that the epidermal features are for the most part obscure or very uniform, *Philodendron* has features important both before and after drying. The internodes of most appressed-climbing hemiepiphytes are actually broader than long at maturity (Figs. 10, 394, 443), but some species, such as *P. advena* (Fig. 38) and *P. straminicaule* (Fig. 392), have internodes typically longer than broad (though short enough that the plants are not considered scandent). Only nine species in Central America have internodes longer than 25 cm on adult or preadult plants. Alternatively, many species have short internodes, with 33 Central American species having internodes to only 5 cm long or less.

Internode width is somewhat less variable, ranging from less than 3 mm diam. in *P. chirripoense* to 10 cm diam. in *P. gigas*. Only nine additional species (*P. chiriquense*, *P. copense*, *P. dressleri*, *P. fer-*

rugineum, P. fortunense, P. grayumii, P. pterotum, P. schottianum, and *P. warszewiczii*) have stems that attain diameters greater than 7 cm. Most species have relatively narrow internodes, with 44 species having internodes of no more than 3 cm diam., and 16 species with internodes of less than 1.5 cm diam.

Fresh stems often have characteristic surface features. Surfaces are frequently speckled with a lighter or darker pattern of green. The surface may also be short-lineate (Fig. 2) or may present a combination of short lines and speckles (Fig. 3). At other times the surface may be weakly to prominently striate as in *P. anisotomum, P. hederaceum,* and *P. wilburii.* The stems may be glaucous as sometimes in *P. dodsonii, P. fortunense, P. immixtum, P. ligulatum, P. mexicanum,* and *P. wendlandii.* Frequently the internodes are coarsely short-costate (Fig. 2) near the apex of the internode, as in *P. chiriquense, P. grandipes,* and *P. schottianum.* These apparently represent areas at which roots will emerge later.

Stems are commonly smooth but may be minutely wrinkled, as in *P. verrucosum,* or sparsely warty, as in *P. brunneicaule,* or setose, as in *P. jacquinii,* or with often branched, trichome-like scales (Fig. 5), as in *P. brevispathum.* Other species with scaly stems are: *P. hammelii, P. malesevichiae, P. squamicaule, P. squamipetiolatum,* and *P. verrucosum.* Even stems of species with smooth epidermis are often weakly fissured in fresh condition (Fig. 2).

Coloration of fresh stems may also be characteristic; typically, they are medium to dark green when fresh, turning gray-green to brownish, yellow-brown or reddish brown in age. Often several transitional stages are involved, e.g., medium green to gray-green, to yellowish green and finally yellowish or reddish brown. This final stem color is often the same as the color of the stem of artificially dried herbarium collections, but at other times the dried stem color of the herbarium collection is not the same. Thus it may be important to note the color of the fresh stem before drying takes place. Natural aging of the stems often causes a scurfy condition, which results from numerous close cracks (Figs. 4, 5). Sometimes these minute fissures are restricted to a specific point of stress yet not visible elsewhere (Fig. 5).

Another important feature is the extent to which the stem wrinkles or cracks or is otherwise distorted by the drying process. The results of the drying process are usually quite consistent from collection to collection, such that the dried stem and the features it exhibits provide useful recognition characteristics.

Stems commonly dry with irregular (or sometimes regular) ribs and intervening sulcae, reflecting shrinkage of the relatively indurate outer surface of the stem compared to the rather soft, somewhat aerenchymatous stem interior. In some cases the regularity and severity of this ribbing provide especially useful characteristics, e.g., in *P. sulcicaule* the stems of which become prominently ribbed in the course of normal development, and in *P. verapazense* where the stems become regularly and conspicuously ribbed on herbarium collections.

In addition to frequently present longitudinal ribs, in e.g., *P. findens, P. fortunense,* and *P. helleniae,* stems may be transversely fissured or checked with small to large fissures. These may be quite regular or irregular in severity or spacing. While sometimes characteristic, these transverse stem fissures tend to be somewhat less consistent than the longitudinal fissures. However, for some species such as *P. edenudatum, P. ferrugineum, P. findens, P. fortunense, P. ligulatum, P. malesevichiae, P. mexicanum,* and *P. wendlandii* (among others), the stems are frequently transversely fissured. Such stems are particularly noteworthy in an undescribed South American species, i.e., *Croat 62785* from the Pacific coast of Colombia.

Another feature exhibited by some dried stems is an exfoliating epidermis, present in *P. angustilobum, P. cotonense, P. dodsonii, P. hederaceum, P. schottianum, P. smithii, P. straminicaule, P. subincisum,* and *P. tripartitum.* In some cases the epidermis not only cracks but may begin to loosen and fall off or protrude away from the stem (Fig. 8), such as in *P. brevispathum, P. cotonense, P. dodsonii, P. ligulatum,* and *P. purpureoviride.* Occasionally this feature is exhibited on fresh stems as well. This is especially true if the stem is forced to bend by falling from its support, such as in *P. immixtum* and *P. sulcicaule.* The epidermis appears to be hard and brittle, while the underlying stem appears to be green and supple. In some cases the epidermis seems to be naturally shed and replaced by another epidermal layer on the fresh stem.

Petiolar scars. Although less conspicuous in general than in *Anthurium* or in *P.* subg. *Meconostigma,* the petiolar scars on the stems of *P.* subg. *Philodendron* are nonetheless clearly visible unless covered with persisting cataphylls. In contrast to *Anthurium* the petiolar scars of *P.* subg. *Philodendron* are generally much less indented but rather are more or less flush with the general contour of the stem surface. They may be moderately inconspicuous as in *P. rothschuhianum* (Fig. 9) or moderately conspicuous as in *P. davidsonii* (Fig. 10).

Philodendron petioles are typically much swollen at the base, so the scar is usually broader than the rest of the petiole itself. Petiole scars vary from (0.5–)1 to 4(–7.5) cm high and (0.7–)1 to 5(–7) cm diam., but they are rarely more than 3 cm high and 3.5 cm diam. The average height and width for the 32 species studied is 2 cm high and 2.4 cm diam. The peduncular scar is often quite conspicuous (Fig. 5) and deep. Of ecological significance is the fact that these deep holes left when the inflorescences fall off are the points of entry for phytophagous insects, especially stem borers, which infect the older and sometimes the younger portions of the stems.

Intravaginal squamulae (Dahlgren & Clifford, 1982), so prominent in *P.* subg. *Meconostigma*, are usually present but often inconspicuous in *P.* subg. *Philodendron* (Fig. 11). Mayo (1991) stressed this as evidence of differences in two contrasting patterns of stem elongation (see discussion under stem above). In *P.* subg. *Philodendron* the intravaginal squamulae (Fig. 11) are always immediately above the cataphyll (prophyll of Ray, 1987a), whereas in *P.* subg. *Meconostigma* the intravaginal squammulae are immediately below the cataphyll scars and often around the scar for the foliage leaf as well.

Roots. *Philodendron* roots have an anatomically distinct layer of exodermis beneath the epidermis, distinguished, among other things, by a long-cell/short-cell pattern (French, 1987a). "Thick-walled, pitted sclereids form a cylinder adjacent to the endodermis and similar sclereids also occur singly or in bands with suberized cork cells in the periderm of older roots" (French, 1987a). Like those of other members of tribe Philodendreae, *Philodendron* roots have a sclerotic hypodermis. French reported the scelerotic hypodermis to be distinctive because of its position next to the exodermis and its occurrence in the primary axis. Another distinctive anatomical feature of the roots of *Philodendron* is resin canals with sclerotic sheaths (French, 1987a).

All species of *Philodendron* produce adventitious roots at some or all nodes. The number of roots developed seems to have more to do with the environment than with the species involved. Plants that are appressed-climbing and in close contact with the substrate generally produce the largest number of adventitious roots. Roots may be of two types, which differ both morphologically and anatomically (Lierau, 1888; Porsch, 1911), either for anchoring the plant to the substrate or for feeding (van Tieghem, 1907; Went, 1893). The anchor roots (Fig. 54) tend to be more numerous and shorter, often with a dense layer of root hairs (they are sometimes restricted to the side of the root that contacts the substrate). They also have a proportionately much smaller central cylinder and more mechanical tissue to give them strength (Engler & Krause, 1908) than those of feeder roots. They arise principally at the nodes but may arise all along the internodes. Anchoring roots may spread from the nodes as in *P. auriculatum* (Fig. 12) or closely appressed to the surface of the tree on which they are growing as in *P. gigas* (Fig. 13). In contrast to the anchoring roots, the feeder roots (Fig. 14) tend to be much thicker and longer and usually extend toward the ground. This behavior is to be expected since Goebel and Sandt (1930) reported that feeder roots of aroids are negatively heliotropic and positively hydrotropic. Feeder roots have a much broader central cylinder and broader vessels and sieve tubes. Feeder roots arise only at the nodes (Grayum, 1990). Normally, the feeder roots are 2–4 times thicker than the anchor roots, and in *P. gigas* the feeder roots may be somewhat woody and up to 3.5 cm diam.

Some species, such as *P. auriculatum* (Fig. 12), have spine-like branch buds sparsely scattered along the length of the root, especially near the stem. Some hemiepiphytes, such as *P. solimoesense* A. C. Sm. in South America, have roots that may become markedly roughened with warty tubercles. In such cases the only portion of the root that has root hairs is the apex where the roots branch as they near the ground. It is unknown whether these roots are capable of absorbing atmospheric humidity, as is true for some *Anthurium* species, but certainly they must be able to take in the free water that runs down the root.

French (1987a) reported that in *P.* subg. *Philodendron* a sclerotic hypodermis is entirely absent in subterranean roots but present in the aerial roots. *Philodendron* subg. *Philodendron* has elongated, infrequently anastomosing resin canals that extend lengthwise through the root cortex (French, 1987c). They are lined with a layer of epithelial cells that consist of thin-walled, unlignified cells (parenchyma). In *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* the epithelium is surrounded by a sheath with lignified cell walls. In contrast, *P.* subg. *Meconostigma* has resin canal sheaths that lack a sclerenchyma and instead have 2–5 layers of (unlignified) collenchymatous cells, which are easily distinguished from the ground tissue (French, 1987c).

While seldom used taxonomically, roots are variable to some extent from species to species. Fresh root coloration (ranging from whitish to green to brownish), length, diameter, and surface texture

Table 2. Persistent condition of cataphylls by section.

Section	Deciduous		Persisting					
	Total	% of sect.	Intact	Semi-intact	As fibers	Total	% of sect.	Section total
Calostigma	34	69%	6	6	3	15	31%	49
Macrogynium	1	100%	0	0	0	0	0%	1
Philodendron	10	24%	0	18	14	32	76%	42
Polytomium	3	100%	0	0	0	0	0%	3
Tritomophyllum	7	88%	0	1	0	1	13%	8
Total	55	53%	6	25	17	48	47%	103

(smooth, coarse, or even warty), as well as the dried color and degree to which they are fissured or folded, are all features that may be recorded. These features have not been used extensively since the roots are generally removed from the stems before the herbarium specimens are prepared.

Cataphylls. In the taxonomy of *Philodendron* probably no morphological feature is more diagnostic than the cataphyll (sylleptic prophyll of Ray, 1987a). *Philodendron* exhibits considerable variation and remarkable consistency in cataphyll characters. Among the most valuable characters is whether the cataphylls are deciduous or persistent. This is the single feature that makes the preparation of keys to species of *Philodendron* easier than those for *Anthurium.* In *P.* subg. *Philodendron* 56 taxa have deciduous cataphylls, while 48 have persistent cataphylls. Of the latter, 6 have cataphylls that persist intact, 25 have cataphylls that persist semi-intact, and 17 have cataphylls that persist as fibers. While a few species have cataphylls tardily deciduous and others have persistent cataphylls that eventually fall off, relatively few species are difficult to place in one or the other category. See Table 2 for a breakdown of persistent condition of cataphylls by section.

Generally speaking cataphylls are deciduous in vines and persistent on appressed-climbing plants, but there are exceptions in both groups. Cataphylls are bract-like modified leaves which function in the protection of newly emerging leaves. For vines, the cataphyll becomes functionless once the leaf has emerged and generally is promptly deciduous. Typically it recurls away from the stem on vines and eventually becomes loosened from the base and falls free, such as on *P. purpureoviride* (Fig. 320). Alternatively, on epiphytes or appressed-climbing hemiepiphytes with short internodes the cataphylls cannot easily fall free (Figs. 15, 115, 312). Although they may fall free from the stem and invariably promptly dry and usually become withered or weather into fibers, they are often prevented from falling by the tight cluster of petioles generally found on plants with short internodes. They do regularly fall free on some species with short internodes, such as *P. warszewiczii* (Fig. 443) or *P. dressleri* (Fig. 160), but typically cataphylls persist on species with short internodes (Fig. 302, *P. pirrense*; Fig. 358, *P. scalarinerve*). Cataphylls often persist in an organized mass around the apex of the stem (Fig. 382, *P. squamicaule*). They may persist intact in *P. grandipes* (Fig. 204), *P. jodavisianum* (Fig. 248), and *P. roseospathum* (Figs. 341, 343), or have a very thin, flaky epidermis that remains intact in large pieces as in *P. dodsonii, P. hebetatum,* or *P. strictum* (Fig. 398); more frequently they decompose at least partially to expose a network of fibers beneath the epidermis (Fig. 258, *P. lazorii*), and even more frequently the epidermis disappears altogether (Fig. 202, *P. glanduliferum*; Fig. 253, *P. jodavisianum*; Fig. 370. *P. schottianum*). Ecologically the mass of cataphyll fibers serves a useful purpose, namely to prevent desiccation of the stem apex and especially the young roots which emerge through the moist cataphyll mass. In some species the layered cluster of cataphylls forms a sodden mass (Fig. 370, *P. schottianum*; Fig. 63, *P. antonioanum*; Fig. 99, *P. chiriquense*), and in some cases the youngest cataphylls are protected by a gelatinous, mucilaginous fluid that fills the interstices of the cataphyll mass. Cataphylls are generally rigid and firm when fresh, which protects the young leaf from physical damage. Some are thick and fleshy with considerable amounts of liquid in their tissues. As these begin to decompose they may yield large amounts of watery or even gelatinous sap. This fluid may be important as a lubricant for the emerging leaf to prevent damage to the tender tissues or to prevent desiccation. Since epiphytes are often subject to harsh conditions, this is probably important to protect the growing point of the plant and the newly emergent leaves from

extremes in temperature and humidity. Although the cataphylls soon lose their moisture after they have opened, many persist semi-intact or as an organized network of fibers so they continue to add protection to the stem apex. Even after the cataphylls are reduced to a mass of fibers they retain moisture much as a pile of straw does after a rain.

A typical cataphyll is narrowly triangular, 2.3–4 times longer than wide, with the base as broad as the circumference of the stem. It may be more than 1 cm thick toward the base on larger species. Cataphyll size is somewhat proportional to leaf size on any species, ranging from (5–)10 to 50(–70) cm long and (1.5–)2.5 to 18(–31) cm wide. Since the cataphyll is affixed around the complete circumference of the stem and eventually becomes deciduous, it leaves a distinct scar on the stem. These cataphyll scars alternate with the petiolar scars and may be conspicuous (Fig. 10, *P. davidsonii* subsp. *davidsonii*) or inconspicuous (Fig. 9, *P. rothschuhianum*). Fresh cataphylls are usually green, though in some cases almost white, as in *P. wilburii*, bright red, or heavily tinged red on exposed parts, such as in *P. antonioanum*, *P. niqueanum*, and *P. tysonii*, or reddish as in *P. glanduliferum*, *P. grandipes*, and *P. pirrense*. Cataphylls are often variously ribbed. In cross section they are frequently sharply D-shaped in outline but may be subterete. When subterete they may be unribbed or bluntly 1- or 2-ribbed (Fig. 60, *P. annulatum*; Fig. 16, *P. warszewiczii*; Fig. 17, *P. schottianum*) or sharply 1-ribbed. Those cataphylls which are D-shaped are often bluntly to sharply raised along the edges of the flat side so that they appear bluntly to sharply 2-ribbed, as in *P. pseudauriculatum* (Fig. 313). The ribs may be moderately low and closely spaced as in *P. panamense* (Fig. 298). In some cases the ribs are slender and knife-edged and may be as much as 1 cm high, as in *P. auriculatum* (Fig. 72) and *P. annulatum* (Fig. 60).

Useful taxonomic characters are found in the manner in which the cataphylls weather and persist. Cataphylls may be quite distinctive in the degree to which they persist intact or weather to fibers. The coloration of the cataphyll fibers is also variable, with colors ranging from almost white to tan, various shades of brown or yellow to reddish or reddish brown. Cataphylls are often short-lineate in the same manner as the petioles (Fig. 16). Some species have the network of fibers highly organized, while in other species the fibers are very disheveled, such as in *P. tenue* or *P. panamense*. In most species the epidermis of the cataphyll promptly falls off, while in some species all or parts of the epidermis persist. In *P. schottianum* the distinctive yellowish epidermis of the cataphylls is one of the most characteristic features.

In time the lowermost cataphylls simply rot away, even for species with a large cataphyll mass, so that ultimately the oldest part of the stem is visible. By this time the stem is quite old and few visible features are worth noting.

For many species the entire cataphyll does not persist, but rather only the basal part remains. Despite the fact that the stem is not covered with a large cataphyll mass, the stem is not easily visible. In such species the cataphyll bases seem to persist longer than in those cases where the entire cataphyll eventually falls free after persisting for a time.

Leaves. Leaves of *P.* subg. *Philodendron*, like those of *P.* sect. *Meconostigma* and *P.* sect. *Pteromischum* (indeed, most Araceae), have supervolute vernation (Cullen, 1978). Like most other aroids, *Philodendron* leaves undergo heteroblastic development, a gradual change in morphology from juvenile to adult forms (Grayum, 1990). However, heteroblasty in *P.* subg. *Philodendron* is not so severe as in other Araceae, especially in subfamilies Lasioideae and Monsteroideae. Typically, the juvenile blades are not dramatically different from those of the adults; commonly they are of similar shape as the adult blades, typically ovate to oblong, and virtually always lack posterior lobes. In rare cases, such as with *P. hederaceum* var. *kirkbridei* (Fig. 223), the juvenile blades are velvety, a feature that is caused by the markedly convex or even somewhat cone-shaped epidermal cells. Ecologically, this lack of glossiness has the effect of allowing nearly all light that falls on the leaf to be absorbed. In all but a few species, notably *P. gigas*, the velvety juvenile leaves are transformed to glossy or semiglossy adult leaves.

In terms of adult blade shape *P.* subg. *Philodendron* is exceedingly diverse, encompassing more morphological variation than is exhibited in *P.* subg. *Meconostigma* or *P.* subg. *Pteromischum* and indeed all the variation exhibited in the much larger genus *Anthurium*. Leaves are typically clustered at the end of the stem, and rarely more than ten are present at a time. Older leaves are eventually deciduous, falling free along with the petiole. In some rare cases the blades fall free first, followed by the somewhat more persistent petioles. The resulting petiolar scar (discussed above under stem) may not be apparent initially on species with persistent cataphylls, but even in these cases they are typically apparent on the older stems. Still, they are never so conspicuous as the petiolar scars in *P.* subg. *Meconostigma*.

In his review of leaf morphology and function Ray (1987a) divided leaves into three main types: foliage leaves, reduced leaves (10–70% the size of the foliage leaves), and cataphylls (reduced to less than 10% of a foliage leaf). The first leaf on a vegetative axis he refers to as a prophyll (in *Philodendron* always a cataphyll). This structure is usually 2-ribbed and is in this regard similar to the bracts that subtend inflorescences. The latter are referred to as bracteoles by Ray (1987a).

The leaf immediately following the prophyll is a fully developed leaf, referred to as a mesophyll (metaphyll of Grayum, 1986). All three types of leaves mentioned above may be modified by the terms prolepic and sylleptic, depending on the type of growth involved. Sympodial growth has petioles borne on the side of the stem, whereas monopodial growth has conspicuously sheathed petioles that encircle the stem. Any leaf subtending an inflorescence or an aborted inflorescence primordium is termed a sympodial leaf (Ray, 1987a). In *P.* subg. *Philodendron* all adult leaves are of this type. Juvenile leaves of *P.* subg. *Philodendron*, on the other hand, are all monopodial leaves (Grayum, 1990).

Petioles. Petioles of *P.* subg. *Philodendron* are usually elongated, sheathed only at the base in adult foliage and rarely with a conspicuous geniculum. Most species have blades as long as or longer than the petioles, but 63 species have blades at least sometimes shorter than the petioles. Twenty-one species have petioles reported as being as long as the blades, while 93 taxa have blades at least sometimes longer than the petioles. Petioles range in length from 4 cm in *P. bakeri* to 137 cm in *P. gigas*. Twenty-two species have petioles always less than 30 cm long, 11 less than 20 cm long, and only 4 species, namely *P. bakeri*, *P. brewsterense*, *P. chirripoense*, and *P. ubigantupense*, have petioles less than 15 cm long. Four taxa, *P. copense*, *P. radiatum* var. *radiatum*, *P. chiriquense*, and *P. tenue*, have petioles more than 1 m long.

Petioles range from less than 5 mm diam. on fresh petioles of *P. brewsterense* to ca. 7.5 cm diam. on *P. wendlandii* and *P. radiatum*.

Usually the petioles are erect-spreading from the stem with the blades either extending initially in the same plane or, more frequently, somewhat pendent from the end of the petiole.

Petiole cross section is not so variable in shape as in *Anthurium*, but the variation is important taxonomically. All too often herbarium collections make no mention of this frequently critical diagnostic feature. Typically petioles are obtusely somewhat flattened or sometimes broadly and obtusely sulcate at the base (Fig. 212). In either event they typically become more terete toward the middle and then obtusely somewhat flattened toward the apex (Fig. 18). Frequently also the petiole has an obtuse medial rib toward the apex where it becomes somewhat flattened.

The majority of *Philodendron* species have terete or subterete petioles. Sometimes the petioles are C-shaped, that is, subterete, yet also sharply adaxially sulcate. Forty-six taxa are described as having petioles subterete in cross section. Some species have subterete petioles with the adaxial surface also narrowly and obtusely sulcate as in *P. cretosum* (Fig. 126), *P. jacquinii*, *P. roseospathum*, and sometimes in *P. sagittifolium*.

Twenty-one Central American species of *P.* subg. *Philodendron* are described as having petioles variously D-shaped in cross section. Examples of species with D-shaped petioles are: *P. copense*, *P. findens*, *P. fortunense*, *P. fragrantissimum* (Fig. 187), *P. grandipes*, *P. jodavisianum*, *P. knappiae*, *P. lentii* (Fig. 264), *P. ligulatum* var. *heraclioanum* (Figs. 275, 276), *P. thalassicum*, and *P. verapazense*. Petioles of *Philodendron advena*, *P. pterotum*, *P. immixtum*, and *P. ligulatum* var. *ovatum* are also sometimes sharply flattened adaxially. Considerable variation exists in petioles described as D-shaped in cross section. Several species have petioles broadly and sharply sulcate, e.g., *P. bakeri*, *P. davidsonii*, *P. heleniae*, *P. lentii* (Fig. 264), *P. ligulatum*, *P. jodavisianum*, and *P. scalarinerve*. Rarely the adaxial surface is sharply and broadly concave and with the petiole often much broader than thick, as in *P. wendlandii* (Fig. 453). In the latter, the lateral margins may be very acute and directed outward. D-shaped petioles generally have the lateral margins weakly to prominently raised with the marginal rib either acute or obtuse. Taxa with the petiole margins acute comprise: *P. davidsonii*, *P. ligulatum* var. *heraclioanum*, and *P. wendlandii*. They are sometimes also acute on *P. chiriquense*, *P. llanense*, and *P. warszewiczii*. Sometimes, as in *P. findens*, *P. fortunense*, and *P. pterotum*, the margins are prominently winged. The wing is erect-spreading and may be markedly undulate in the area of the geniculum as in *P. fortunense* (Fig. 183) and *P. findens* (Fig. 171). Sometimes the petioles of *P. ligulatum* var. *heraclioanum* also may be weakly winged (Figs. 275, 276). Even petioles not D-shaped often have a slightly thickened, slightly raised lateral margin on the adaxial surface. Examples include *P. annulatum*, *P. cretosum*, *P. microstictum*, *P. thalassicum*, and *P. wilburii*.

Sometimes in addition to the raised margins of the petioles, there may be a prominent medial rib,

such as in *P. jodavisianum* and occasionally *P. grandipes*, giving the petiole a three-ribbed appearance adaxially. More commonly the medial rib is broad and obtuse, such as in *P. angustilobum*, *P. annulatum*, *P. copense*, *P. crassispathum*, *P. ferrugineum*, *P. ligulatum*, *P. llanense*, *P. schottianum*, *P. smithii*, *P. tenue*, *P. thalassicum*, and *P. tripartitum*.

Rarely the petioles may be markedly flattened dorso-ventrally, as in *P. platypetiolatum*. In this case the petioles are much broader than thick with the lateral margins nearly acute.

A few species have petioles markedly thicker than broad and U-shaped in cross section. Examples include *P. roseospathum*, *P. jodavisianum*, and sometimes *P. davidsonii*. Petioles of the latter species are more commonly obtusely V-shaped in cross section.

Petioles of *P.* subg. *Philodendron* typically have very short sheaths when the inflorescence is aborted and much longer sheaths (to accommodate the emerging inflorescences) when subtending an inflorecence (Figs. 38, 67, 93, 150). Generally the sheath is markedly closed with one margin overlapping the other, making it inconspicuous (Figs. 83, 160). Occasionally the petiole sheath may be conspicuous, such as in *P. correae* (Fig. 119) and some members of *P.* subsect. *Glossophyllum*.

A geniculum is typically not apparent, but the genicular area serves the same purpose as it does in *Anthurium*. It is involved with inclining or twisting the plane of the blade, presumably optimizing exposure to sunlight. Usually the genicular area is somewhat firmer than the remainder of the petiole, and sometimes it is differently colored, but it is usually neither swollen nor as conspicuously distinct as in *Anthurium*. Typically the genicular area is the same shape as the remainder of the petiole, but sometimes the cross-sectional shape is different, being more frequently bluntly ribbed and often rather deeply cracked or scurfy around the circumference (perhaps owing to the bending in response to light). The geniculum, when apparent, is sometimes thicker than the remainder of the petiole as in *P. brunneicaule*, *P. ferrugineum*, *P. heleniae*, and *P. tenue*. It may be darker than the petiole as sometimes in *P. bakeri* or *P. glanduliferum*, or slightly paler as in *P. ferrugineum* or *P. scalarinerve*.

Most species of *Philodendron*, like Araceae in general, have glabrous petioles, but there are conspicuous exceptions. Several species have conspicuously scaly petioles: *P. hammelii*, *P. glanduliferum*, *P. malesevichiae* (Fig. 283), *P. squamipetiolatum* (Fig. 387), *P. squamicaule* (Fig. 382), and *P. verrucosum*. The type of scales is also variable. In some species, such as *P. malesevichiae*, *P. glanduliferum*, and *P. squamipetiolatum*, the scales are acicular and more or less terete. The scales of *P. glanduliferum* and *P. malesevichiae* are spreading, while those of *P. squamipetiolatum* are sometimes retrorse near the apex of the petiole. In addition, they are densely granular-scurfy on the surface. In *P. hammelii* the scales are short and broadened laterally, similar to fish scales, and less than three times longer than broad. In *P. verrucosum* and *P. squamicaule* the scales are of two distinct types. *Philodendron verrucosum* has short, broad, and often lacerate scales interspersed with long-acicular scales. *Philodendron squamicaule* has short, purplish, deltoid, broader than high (about 2 mm high) scales interspersed among acicular, greenish scales 3–5 mm long.

Petiolar scales are not uniformly distributed along the petioles. In *P. squamipetiolatum*, *P. squamicaule*, and *P. verrucosum* the scales are usually scattered throughout the petioles. In *P. malesevichiae* they are present in the upper ½ to ⅓ of the petioles, becoming increasingly denser toward the base. In *P. glanduliferum* they are similar but more closely aggregated toward the apex. In *P. hammelii* the scales are restricted to a small area near the apex. *Philodendron ornatum* in South America is the most extreme example of this reduction. In that species the scales are reduced to stubby protuberances restricted to the apex of the petiole.

Surface features of both fresh and dried petioles are often conspicuous and frequently diagnostic. Though usually solid green, petioles may be irregularly purplish-spotted as in *P. edenudatum* (Fig. 163) and *P. sagittifolium*. This purplish spotting may continue onto the lower midrib, a feature common to other types of markings that continue onto at least the proximal portions of the midrib. The surfaces of petioles may be minutely speckled but more commonly bear a light pattern of short dashes or streaks usually uniformly distributed throughout the petiole. They may be densely to sparsely marked with short dashes, which in turn may be either darker or lighter than the surface. I have referred to this feature in the descriptions as "short-lineate" or "lineate." Though the lineations are usually short, usually less than 3 mm long, they may sometimes be longer and sometimes are variable in length with both short and long lines interspersed (Fig. 19). Examples of species with short-lineate petioles include: *P. annulatum*, *P. auriculatum*, *P. copense*, *P. cotonense*, *P. edenudatum*, *P. fortunense*, *P. immixtum*, *P. ligulatum*, *P. pirrense*, *P. purulhense*, *P. smithii*, *P. subincisum*, *P. thalassicum*, *P. warszewiczii*, and *P. zhuanum*. The peti-

oles of *P. brunneicaule* are red short-lineate. The short lineations may be associated as well with much longer, continuous, and frequently weakly raised striations or ribs. Species with petioles described as short-lineate to striate include: *P. antonioanum, P. clewellii, P. gigas, P. glanduliferum,* and *P. panamense.* Still other species have more or less continuous striations throughout: e.g., *P. anisotomum, P. davidsonii, P. dressleri, P. findens, P. madronense, P. rothschuhianum, P. straminicaule, P. tenue,* and *P. warszewiczii.*

Fresh petioles of *P.* subsect. *Glossophyllum* usually have a distinct purplish (or rarely dark green) ring (Fig. 20) around the entire petiole just below its junction with the blade. The species that share this feature, mostly members of *P.* subsect. *Glossophyllum,* include *P. annulatum* (Fig. 59), *P. bakeri, P. correae,* and *P. ligulatum* (all three varieties; see Figs. 271, 275) with a purplish or purple-black ring, and *P. auriculatum* (Fig. 20), *P. immixtum, P. dolichophyllum, P. pseudauriculatum,* and *P. wendlandii* with a dark green ring at the apex of the petiole.

Other apparently unrelated species may likewise have purple rings around the apexes of the petioles. These include *P. brenesii, P. davidsonii, P. dressleri, P. ferrugineum, P. microstictum, P. smithii, P. warszewiczii,* and sometimes *P. grayumii.*

Petioles may produce a cluster of viscid droplets of a sweet, sugary solution on the abaxial surface at the apex of the youngest leaves. This has been observed on *P. davidsonii* subsp. *bocatoranum* (Fig. 19) and *P. megalophyllum* Schott, a common South American species. These droplets appear to have no function in pollination or in blade orientation, and I speculate that they act as a food source for ant guards, which serve to prevent the young blades from predation by phytophagous insects. This seems all the more likely because the droplets are associated with new leaves, which are typically very tender and thus most easily damaged.

Freshly cut petioles usually form resin droplets in the same manner as the stems, and may in time become completely covered with resin. Of rare occurrence are slender strands of latex on broken and partially severed petioles as on *P. malesevichiae* (Fig. 21).

Dried petioles yield another suite of characteristics generally unrelated to those exhibited on fresh plants.

The dried petiole is sometimes diagnostic and in some cases, such as *P. hebetatum* and *P. schottianum,* petioles have a dried epidermis that is so conspicuously yellow-brown as to be nearly unique. Though less conspicuous, the petioles of *P. schottianum* and *P. thalassicum* also dry quite yellowish brown.

Petiole firmness is variable in *P.* subg. *Philodendron,* but this character is difficult to quantify. Unfortunately Engler used this character as one of his major key characters to separate subsections of *P.* sect. *Cardiobelium, P.* subsect. *Macrobelium,* and *P.* subsect. *Glossophyllum* with very fleshy petioles from *P.* Gruppe *Oligocarpidium,* and *P.* Gruppe *Doratophyllum* (now *P.* subsect. *Bulaoana*) with firm petioles. This character is difficult to describe and petioles appear to range from quite firm to quite spongy without any major discontinuities. Most species have petioles firm to weakly spongy when squeezed, and generally they are quite flexible, capable of being bent to a great extent without breaking. However, spongy petioles, such as those in *P. ligulatum* which can be easily crushed by squeezing, are also more likely to be brittle.

Blades. Blade shape. Virtually the entire range of morphological variation in leaf shape in the genus as a whole is exhibited among the Central American species of *P.* subg. *Philodendron.* The only blade shapes of *Philodendron* not shown by Central American species are those seen on *P. goeldii* G. Barroso in *P.* subg. *Meconostigma,* which has blades reniform in outline and pedately compound, and members of *P.* sect. *Schizoplacium,* which have blades pinnately lobed with a few, prominently falcate divisions. While *P.* subg. *Pteromischum* has distinctive leaves (even discounting the winged petiole on adult plants, which is definitive), their overall shape and size is matched by some other species of *P.* subg. *Philodendron.* Blade shape in *P.* subg. *Philodendron* relates in some cases to sectional differences. For example, species with three-lobed blades are either members of *P.* sect. *Tritomophyllum* or *P.* subsect. *Bulaoana.* Pinnately lobed species are members of *P.* sect. *Polytomium.* Some sections, especially *P.* sect. *Philodendron* and *P.* sect. *Calostigma,* are highly variable in blade shape, with that of *P.* sect. *Philodendron* ranging from oblong to variously ovate to ovate-sagittate and that of *P.* sect. *Calostigma* ranging from oblong to subcordate, prominently cordate, cordate-sagittate, or even 3-lobed. *Philodendron* subsect. *Glossophyllum,* relatively common in Central America, has more or less oblong, frequently subcordate or cordulate blades. See also section on "Discussion of Subgeneric Classification" for additional details.

While lobed leaves in some Araceae, e.g., *Monstera,* are due to necrotic processes in which growth stops and tissue rots away (Madison, 1977), the

lobed leaves of *Philodendron* are due to differential growth of leaf tissue.

In Central America more species have ovate-cordate blades than any other shape. In all variations, 38 species have some sort of ovate-cordate leaf blade. Twenty-two species are described as having ovate-cordate blades, and 11 as broadly cordate. Species with ovate to ovate-triangular leaves are most abundant among *P.* subg. *Philodendron* in Central America. At least 55 species have leaf blades with well-developed posterior lobes, including cordate, sagittate, and hastate. Only 15 species have non-cordate blades prominently longer than wide. Eight species have lobed blades, six trilobed, and two pinnately lobed. Species with trilobed leaves are: *P. anisotomum, P. cotobrusense, P. madronense, P. rothschuhianum, P. tripartitum,* and *P. angustilobum.* Species with pinnately lobed leaves are: *P. radiatum* and *P. warszewiczii.*

Posterior lobes. *Philodendron* subg. *Philodendron* species vary greatly in the shape of posterior lobes: usually rounded for those species with cordate leaf bases, e.g., *P. glanduliferum* (Fig. 197) or *P. platypetiolatum* (Fig. 306), or cordulate[12] leaf bases, e.g., *P. auriculatum* (Fig. 69), *P. immixtum* (Fig. 236), and *P. pseudauriculatum* (Fig. 314); to more or less oblong to narrowly triangular and much longer than wide as in *P. verapazense* (Fig. 434), or sometimes in *P. sagittifolium* (Fig. 346) and *P. tenue* (Fig. 404). Even in species with well-developed posterior lobes the lobes may be about as long as broad, as in *P. purulhense* (Fig. 322), *P. tysonii* (Fig. 426), or *P. schottianum* (Fig. 365). Posterior lobes may be sagittate as in *P. brunneicaule* (Fig. 95), *P. hebetatum* (Fig. 218), or *P. gigas* (Fig. 194); to hastate as in *P. angustilobum* (Fig. 49), *P. anisotomum* (Fig. 55), and *P. mexicanum* (Fig. 287); or bluntly triangular as in *P. wilburii* var. *longipedunculatum* (Fig. 461).

Sinus shape. *Philodendron* species with posterior lobes have remarkable variation in the shape of the sinus: merely arcuate, in *P. microstictum* (Fig. 289); arcuate with decurrent petioles in *P. morii* (Fig. 292); V-shaped in *P. glanduliferum* (Fig. 200), *P. lentii* (Fig. 263), *P. squamipetiolatum* (Fig. 386), and *P. tenue* (Fig. 406); oblong in *P. dwyeri* (Fig. 155); spathulate in *P. basii* (Fig. 76), *P. hebetatum* (Fig. 218), *P. smithii* (Fig. 372), and *P. rothschuhianum* (Fig. 339); parabolic in *P. sulcicaule*; hippocrepiform in *P. hebetatum* (Fig. 225), *P. lazorii, P. panamense* (Fig. 297), and *P. squamicaule* (Fig. 374); sometimes closed on live plants as in *P. fortunense* (Fig. 182), *P. gigas* (Fig. 194), *P. pterotum* (Fig. 311), and *P. schottianum* (Fig. 366). In *P. fortunense* and *P. subincisum* (Fig. 401) the sinus may be closed even on pressed plants. The shape of the sinus varies greatly between live and flattened dried plants, since the shape of the sinus varies depending on the angle at which the posterior lobes are turned up in relation to the midrib. Many species have the posterior lobes turned upward at an angle to the midrib on live plants (see, e.g., Figs. 104, 130, 159, 186, 366, 374), causing the inner margins of the posterior lobes to become closer to each other and thus decreasing the apparent size of the sinus. For example, when the angle of the posterior lobes is extreme the posterior lobes might be closed, but when the same blade is flattened and dried the sinus might become spathulate or hippocrepiform. The description of the sinus as presented in this work for Central American *P.* subg. *Philodendron* is exclusively that of the flattened sinus unless otherwise stated.

The sinus shape may be intraspecifically variable as in *P. sousae,* for example, with the sinus ranging from spathulate (Fig. 379) to parabolic (Fig. 380). This is in part related to the age of the plant, with older plants bearing larger blades that have larger, more well developed posterior lobes.

Blade size. Blades of *P.* subg. *Philodendron* in Central America as elsewhere are highly variable in size, but relatively few have blades that are considered huge. Only 19 Central American species of *P.* subg. *Philodendron* have blades that exceed 75 cm long (although many others approach that size). Of these, only *P. gigas* has blades that regularly exceed 1 m in length, with the maximum recorded at 137 cm. The blades of *Philodendron ferrugineum* may rarely exceed 1 m in length. By the same token few species in Central America have small leaves. Only 37 species have blades less than 25 cm long on adult plants, and of these only 13 have blades less than 15 cm long. *Philodendron brewsterense,* with blades a maximum of 11 cm long, is the species with the smallest leaves, and *P. chirripoense,* with blades up to 11.6 cm long, has leaves about as small. The median leaf length for *Philodendron* in Central America is 57 cm.

The widest blades belong to *P. gigas* and *P. radiatum* (to 90 cm long), but *P. pterotum* (to 84 cm wide), *P. findens* (to 70 cm wide), *P. dodsonii* (to 66

[12] With miniature lobes held very near the petiole (see photos of *P. auriculatum*) as compared to subcordate, wherein the lobes, though short, are usually broadly rounded with each lobe encompassing about half the width of the entire blade.

cm), *P. schottianum* (to 64 cm), and *P. warszewiczii* (to 62 cm) also have quite broad blades.

While blade size of *Philodendron* is often not reliable for taxonomic separation and even blade shape is sometimes unreliable, the length-width ratio is, in general, more reliable as a taxonomic character. Blades range from being much broader than long, to more than eight times longer than broad (in *P. cretosum*), to broader than long. Blades are broader than long in a number of species, e.g., averaging only 0.62 times as long as broad in *P. anisotomum* and *P. brunneicaule* and 0.7 times as long as broad in *P. cotobrusense* and *P. grayumii*. The average blade length-width ratio for species with simple, unlobed leaves ranges from 1.6 to 2.5 times longer than wide. Exceptions include *P. cretosum* and *P. folsomii* (8.3 and 5.2 times, respectively).

Blade margins are typically entire on simple leaves, never toothed and only rarely sinuate, such as in *P. subincisum*. Species with weakly sinuate blades are: *P. basii*, *P. dwyeri*, and *P. jefense*. On the other hand, blade margins are frequently undulate to a certain extent, especially on larger blades. Species that have coarsely undulate leaves are: *P. annulatum*, *P. antonioanum*, *P. copense*, *P. ferrugineum*, *P. fortunense*, *P. grandipes*, *P. hebetatum*, *P. panamense*, and *P. sulcicaule*.

Blade margins are frequently hyaline and also often weakly revolute. Examples of species with hyaline blade margins are: *P. advena*, *P. crassispathum*, *P. davidsonii*, *P. ferrugineum*, *P. gigas*, *P. immixtum*, *P. hederaceum*, *P. smithii*, *P. squamicaule*, *P. straminicaule*, *P. subincisum*, and *P. wilburii* var. *longipedunculatum*.

The coloration of leaf blades is highly variable and largely dependent on the habitat, but some species, such as *P. roseospathum*, *P. scalarinerve*, and *P. tysonii*, have very dark green blades while others (e.g., *P. lazorii*) have lighter green blades. A few species, such as *P. chiriquense*, have purple coloration on young leaf blades but most lose this coloration in age. An exception is *P. verrucosum*, which has adult blades generally purplish on the lower surface. A few taxa such as *P. ligulatum* var. *heraclioanum* (Fig. 274) and *P. sagittifolium* have leaf blades purplish-spotted on the lower surface, especially when young. Coloration of lower blade surfaces is more often restricted to the major veins, which are frequently reddish (along with the young petiole) as, for example, in *P. antonioanum*.

Venation. Midribs. Leaf midribs of *P.* subg. *Philodendron* are more variable in cross-sectional shape than those of other aroid genera, such as *Stenospermation*, *Rhodospatha*, *Spathiphyllum*, and *Monstera*, yet not as taxonomically significant as in the related genus *Dieffenbachia*.

Midribs on the upper (adaxial) blade surface of *P.* subg. *Philodendron* are highly variable, being flattened or variously sunken or raised (sometimes even in the same species). Fifty-six species have adaxial midribs at least sometimes raised, 26 have upper midribs at least sometimes sunken (only *P. cretosum* has a deeply sunken midrib), and 54 have adaxial midribs sometimes flat. Only 12 taxa, *P. antonioanum*, *P. aromaticum*, *P. albisuccus*, *P. coloradense*, *P. dressleri*, *P. granulare*, *P. pirrense*, *P. purulhense*, *P. strictum*, *P. warszewiczii*, *P. wilburii* var. *longipedunculatum*, and *P. zhuanum*, are described as having strictly flattened adaxial midribs. Fifteen species are described as having only convex midribs, and 15 are described as having only sunken midribs. Only 2 species, *P. morii* and *P. niqueanum*, are described as having the adaxial midribs prominently raised.

The adaxial midrib is nearly always to some extent paler than the surface. In only 12 species are the midrib and the blade concolorous. An additional 8 species have midribs concolorous to slightly paler.

The lower (abaxial) midrib of *Philodendron* blades exhibits less variability. All species have adaxial midribs to some extent raised. A few species, e.g., *P. crassispathum*, have the abaxial midrib so broadly convex as to appear nearly flat, but most species have the midrib noticeably raised. The abaxial midrib is generally convex but often narrowly rounded, thicker than broad, and sometimes bluntly acute. Species with the abaxial midrib weakly raised are rare in *P.* subg. *Philodendron*. Only seven species have abaxial midribs at least sometimes described as broadly convex or weakly raised: *P. anisotomum*, *P. crassispathum*, *P. fortunense*, *P. microstictum*, *P. platypetiolatum*, *P. purpureoviride*, and *P. straminicaule*.

Many more species have abaxial midribs more prominently raised. In the largest category, 47 species have abaxial midribs more or less convex, i.e., more or less hemispherical in cross section. Thirty-six species have abaxial midribs described as thicker than broad, narrowly convex, narrowly rounded or bluntly acute at least part of the time. A number of these species have abaxial midribs so prominently raised as to be noticeably thicker than broad: *P. copense*, *P. cretosum*, *P. dolichophyllum*, *P. hebetatum*, *P. heleniae*, *P. jodavisianum*, *P. panamense*, and *P. roseospathum*. Taxa that have abaxial midribs sometimes thicker than broad are *P. scalarinerve* and *P. wilburii* var. *longipedunculatum*.

The most extreme type of raised adaxial midribs

is so raised as to appear to be a cylinder attached tangentially to the surface of the leaf. This type of midrib has been referred to as "round-raised." Examples of species with such midribs are *P. brunneicaule, P. dressleri, P. madronense, P. squamipetiolatum,* and *P. radiatum.* In cases where the midrib is round-raised, the primary lateral veins are also sometimes round-raised.

While the abaxial midrib is more likely than the adaxial midrib to be concolorous with the rest of the blade or darker than the remaining blade surface, 45 species still are reported as having the midrib paler than the surface. Twenty-four species have the abaxial midrib described as darker than the surface.

A number of species, including *P. edenudatum, P. grayumii, P. ligulatum* var. *ligulatum,* and *P. sagittifolium,* have one or both midribs maroon- or purplish-spotted.

Primary lateral veins. The primary lateral veins (referred to by some authors as "secondary veins") are those that branch off the midrib and extend to the margins usually without additional branching. This use of primary lateral vein is consistent with that of early aroid workers Engler, Krause, and Sodiro. Engler and later Krause referred to the primary lateral veins as "nervis primariis." Sodiro also referred to the primary lateral veins as "nervis lateralibus I."

On larger cordate blades there is frequent branching of the primary lateral veins in the lower part of the blade where primary lateral veins are widely spaced (Fig. 26) (see also Croat & Bunting, 1979). The presence of these veins, referred to here as "secondary veins," is not commonly indicated in this work, but in shape and aspect they are virtually the same as the primary lateral veins (Fig. 24).

Both surfaces of the blade typically have primary lateral veins similar to the associated midrib. Usually they are somewhat less prominently raised than the midrib. The primary lateral veins on the upper (adaxial) surface, while usually sunken, may be essentially flat with the surface. Sometimes they are raised but at the same time contained within a broad or narrow valley so that the veins appear to be sunken. Primary lateral veins may sometimes be "quilted" (Figs. 23, 200, 361), i.e., with the veins deeply sunken and with the intervening leaf tissue of the blade that lies between the primary lateral veins being broadly raised, making the surface appear like that of a plush quilt.

Primary lateral veins of *P.* subg. *Philodendron* are rarely either absent or so inconspicuous as to appear to be absent, such as in *P. brewsterense,* though they are sometimes not at all conspicuous, as in *P. microstictum* (Fig. 289) or *P. sulcicaule* (Fig. 403). The number of primary lateral veins varies from 2 pairs in *P. chirripoense* to 25 pairs in *P. madronense.* Most species have 3 to 6 pairs of primary lateral veins. These generally arise at an acute angle with the midrib and, after extending along or near the midrib, spread at an angle of generally 40–80° toward the margins, generally forming a broad arc in the process. The angle of primary lateral veins for all species may be as little as 5° to as much as 100°. When species of Central American *P.* subg. *Philodendron* are divided into a series of range categories based on the angle of their primary lateral veins, more species (eight) have primary lateral veins spreading at 50°–60° angle or at 60°–70° (also eight species) than any other group.

Basal veins. Primary lateral veins that contact the plexus at the base of the blade and the apex of the petiole are here referred to as "basal veins" (Fig. 22) (see also Croat & Bunting, 1979). While the uppermost 1 or 2 pairs usually extend upward and into the anterior lobe where they join the antemarginal vein, most extend into the posterior lobes. Generally, basal veins are best developed on plants that have posterior lobes and are not present, or at least are few in number, when the blade lacks posterior lobes. Basal veins, like the primary lateral veins, are typically paired, with usually an equal number on either side of the midrib.

Seventy-three species (75 taxa) of *P.* subg. *Philodendron* in Central America have basal veins. The number of pairs of basal veins ranges from 1 to 15, but only eight species (*P. angustilobum, P. copense* (to 15), *P. findens, P. grandipes, P. thalassicum, P. pirrense, P. squamicaule,* and *P. strictum*) have 10 or more pairs. Most species have 3–6 pairs of basal veins, though up to 16 species may have only 2 pairs of basal veins. Only three species, namely *P. lentii, P. mexicanum,* and *P. scalarinerve,* regularly may have a solitary pair of basal veins.

Posterior ribs. The basal veins are generally to some extent coalesced near their union with the petiole. The union or coalescence of basal veins is here referred to as the "posterior rib" (Figs. 22, 25) (see also Croat & Bunting, 1979). Sixty-three species (65 taxa) have the basal veins at least in part united and thus possess posterior ribs, while 34 species (38 taxa) have the basal veins free to the base (or lack basal veins all together) and thus lack posterior ribs. Both the number and nature of basal veins and the length of the posterior rib are good characters for distinguishing taxa. The basal veins

may be completely coalesced for a distance (Fig. 22) or loosely coalesced. The posterior rib may be prominently naked for a distance (Figs. 22, 169) or barely (Figs. 26, 211) or not at all naked (Figs. 161, 163, 287). The basal veins are free or nearly so in most species with rounded or cordulate leaf bases (Fig. 20). Such species are: *P. auriculatum, P. bakeri, P. correae, P. chirripoense, P. cretosum, P. dolichophyllum, P. granulare, P. immixtum, P. lentii, P. ligulatum, P. pseudauriculatum, P. roseospathum, P. scalarinerve, P. ubigantupense, P. utleyanum,* and *P. wendlandii.* Even species with short or poorly developed posterior lobes, such as *P. annulatum, P. clewellii, P. davidsonii, P. microstictum, P. niqueanum,* and *P. platypetiolatum* usually have the basal veins free to the base. On the other hand, species with well-developed posterior lobes usually have the basal veins coalesced to some degree. Posterior ribs range from less than 0.5 cm long (in *P. straminicaule*) and 1 cm long (in *P. angustilobum, P. basii,* and *P. alticola*) to more than 14 cm long in *P. gigas.*

Another important taxonomic character is the extent to which the posterior rib is naked along the sinus. In general, the longer the posterior rib the more likely it is to be naked at least to some extent along the sinus. However, *P. tenue* is exceptional in having a well-developed posterior rib and being not naked along the sinus. The degree to which the posterior rib is naked along the sinus varies from as little as 0.5 cm in *P. straminicaule* to 6 cm in *P. squamicaule.* Examples of species with prominently naked posterior ribs are: *P. albisuccus, P. alticola, P. aromaticum, P. basii, P. brunneicaule, P. copense, P. dodsonii, P. dressleri, P. findens, P. hebetatum, P. knappiae, P. panamense, P. purulhense, P. strictum, P. thalassicum,* and *P. verapazense.*

Lesser order veins. Between successive primary lateral veins there are possibilities for two additional orders of veins. Frequently present are intermediate primary lateral veins here called "interprimary veins" (Figs. 24, 26) (see also Croat & Bunting, 1979). These veins, while decidedly less conspicuous than the primary lateral veins, are nevertheless too prominent to be classified as the smallest-order veins. To qualify as an interprimary, the vein must extend continuously from the midrib to very near the margin without major branching. Generally there is no more than one pair of interprimary veins between alternate primary lateral veins. They are akin to the primary lateral veins in all aspects except for their reduced size. Like the primary lateral veins they may bear minor veins, which may form all along their margins.

The smallest-order veins are here referred to as "minor veins" (Fig. 24) and may be close, fine, and conspicuous as in *P. sulcicaule, P. tripartitum,* and *P. radiatum,* to thick, well-spaced, and inconspicuous in *P. gigas, P. granulare, P. grayumii,* and *P. ligulatum.* The minor veins are not all equally distinct and sometimes, as in *P. dominicalense,* the minor veins are alternately weakly visible and strongly visible.

The minor veins may arise from the midrib or from the primary lateral and interprimary veins, but in either case they form a generally close, uniform, and parallel array, which extends without interruption to near the margin of the blade. In most species the minor veins arise from both the midrib and the primary lateral veins, but some species have the minor veins arising from only the midrib. A total of 77 species (81 taxa) have the minor veins arising from both the midrib and the primary lateral veins (Fig. 26). In such cases the minor veins are not always equally arising from one of the two entities but may, as in the case of *P. brenesii, P. davidsonii* subsp. *davidsonii, P. ferrugineum,* and *P. tripartitum,* be more heavily arising from the midrib rather than the primary lateral veins. In *P. auriculatum, P. glanduliferum, P. lentii,* and *P. ligulatum* the minor veins arising from the primary lateral veins are many fewer than those arising from the midrib. In *P. heleniae* the primary lateral veins are only rarely arising from the midrib.

In another variation of this venation type, some species, while having minor veins arising from the midrib as well as both adjacent primary lateral veins, have considerably more veins arising from the distal primary lateral vein than from the proximal vein.

A total of 24 species have the minor veins arising from only the midrib, and in this case they course along the primary lateral veins but do not join with it. Many of the species that have the minor veins arising only from the midrib are species with oblong blades, such as: *P. bakeri, P. cretosum, P. dolichophyllum, P. granulare, P. heleniae, P. roseospathum, P. ubigantupense, P. utleyanum,* and *P. wendlandii.* However, this group also has blades ovate or nearly so as in *P. brewsterense, P. chirripoense, P. cotobrusense, P. crassispathum, P. folsomii, P. knappiae, P. microstictum, P. niqueanum, P. sulcicaule,* and *P. verapazense.* Interestingly, *P. anisotomum,* with deeply 3-lobed leaf blades, also has the minor veins arising from only the midrib, whereas *P. tripartitum,* a similar species with 3-lobed blades, has the minor veins arising from both the midrib and the primary lateral veins.

Philodendron dressleri, a species with deeply di-

vided leaves, has a more complex venation pattern. Although the minor veins arise from both the midrib and the primary lateral veins, they also arise from short secondary veins that regularly branch off the primary lateral veins. In addition, the minor veins that arise from the midrib are considerably fewer in number and weaker than in most species with this venation pattern. Generally, the confluent minor veins that arise from the primary lateral veins and make a broad sweep before continuing to the margin leave little area for the minor veins, which arise from the midrib. The latter tend to merge imperceptibly with those from the primary lateral veins. A similar pattern with weak midrib-borne minor veins is present with *P. basii.*

At or very near the margin both the primary lateral veins and the minor veins generally turn sharply toward the apex of the blade. The minor veins join with other minor veins and with the primary veins before finally merging into an inconspicuous and somewhat opaque marginal plexus. This narrow band is usually chlorophyllous and apparently veinless. Frequently the outer margin of this chlorophyllous band is a hyaline edge, which is colorless and typically revolute.

The minor veins are sometimes noticeably interconnected by inconspicuous to conspicuous veins, referred to here as "cross-veins" (Fig. 26). Generally the cross-veins are markedly perpendicular to consecutive minor veins where they are sufficiently prominent to be noticeable, but in some cases the cross-veins cross transversely from one minor vein to the next. While *P. scalarinerve* has cross-veins so prominent, even on fresh material, as to be easily visible, other species such as *P. chiriquense* and *P. copense* have cross-veins easily visible only when the blades are dry.

Secretory ducts and other secretory tissues are frequently present on Central American members of *P.* subg. *Philodendron.* The contents of the secretory ducts are either latex or tanniniferous compounds (Solereder & Meyer, 1928). No thorough survey has been made of the nature of the secretory canals in Central American species, so it is not always apparent whether these structures are resin canals or secretory ducts. Secretory canals (also referred to as secretory files) in *Philodendron* are always non-anastomosing and consist of a linear sequence of secretion cells, each separated from the next by cell walls (Solereder & Meyer, 1928). On fresh and dried leaves these can usually be recognized by being darker, usually blackened, and in being intermittent rather than continuous as is generally true of veins. While the distribution of secretory ducts in *Philodendron* may be more common than is apparent from surface examination, not all species exhibit the secretory ducts clearly. Thus the presence or absence of distinct secretory ducts can be useful taxonomically. They are distinctly visible on *P. alticola, P. cotonense, P. grayumii, P. heleniae,* and *P. zhuanum,* but obscurely visible on *P. antonioanum,* and *P. bakeri.* They are clearly visible on *P. schottianum,* somewhat visible on *P. llanense,* and obscure on *P. findens,* even though these three species have very similar leaf blades.

While perhaps no more reliable than blade shape, blade size, or other features, blade surfaces at a magnification of 10× or higher often reveal another suite of characters, which often yields another degree of confidence (or forewarns of misidentification) when making determinations. The surface between the minor veins is frequently marked by pale sub-surface granulations (perhaps indicating the presence of druse crystals), short, pale lineations, gland-like punctiform markings, reddish or brownish speckling, and also what might be referred to as "stitching," pale intermittent short lines appearing on the surface of the blade as though the blade was loosely sewn with a needle and thread. Though this phenomenon is much more common in *P.* subg. *Pteromischum,* it is also exhibited in *P.* subg. *Philodendron.*

Morphology of Reproductive Structures

Inflorescences

When a plant of *P.* subg. *Philodendron* flowers, the stem apex is terminated by an inflorescence (or frequently an aborted inflorescence primordium) (Ritterbusch, 1971; Blanc, 1977c; Madison, 1978) and new growth is from a bud in the axil of the penultimate leaf. This new growth pushes aside the newly developing leaf and the inflorescence that is developing in its axil (Ray, 1987a). When the inflorescences abort, the petiole sheath remains quite small and unexpanded, but when the inflorescences develop, the sheath may be much larger. *Philodendron* inflorescences are sympodial, with each sympodium consisting of 1–10 (to 11 in South America) inflorescences arising typically in what appears to be the leaf axil of usually one of the upper leaves (but almost never in the uppermost leaf axil). Often inflorescences emerge from the mass of cataphyll fibers, enabling the inflorescence to remain moist (Figs. 63, 115, 188, 371, 430). The individual inflorescences are subtended by and enclosed in a series of moderately coriaceous, whitish to pinkish, 2-ribbed structures (Fig. 195, *P. gigas,* Fig. 428, *P. tysonii*) called bracteoles (Ray, 1987a). These have elsewhere been referred to as prophylls (Usher,

1966; Jackson, 1971). At anthesis the bracteoles are typically deciduous, although sometimes they persist for a time simply because they are held so tightly by the developing infructescences.

Typically the inflorescences are borne in the erect or semi-erect position regardless of the position of the stem. Even when the inflorescence is borne on the end of a pendent stem, the stem usually curves upright so that the opening inflorescence is erect at anthesis (Fig. 273, *P. ligulatum* var. *ovatum*; Fig. 269, *P. ligulatum var. ligulatum*).

The number of inflorescences per axil is taxonomically significant. More species (38) have a solitary inflorescence per axil (or are believed to have a solitary inflorescence) than any other combination. Many others may be found with only a single inflorescence if they are seen in the early stages of flowering or if inflorescences have aborted owing to lack of pollination, but plants frequently have two or more inflorescences per axil later in the flowering season. Careful dissection of the leaf axil usually can provide evidence of the peduncular scar indicating a lost inflorescence. Taxa known to usually have only a single inflorescence per axil are: *P. albisuccus, P. anisotomum, P. aromaticum, P. bakeri, P. basii, P. breedlovei, P. brevispathum, P. brewsterense, P. brunneicaule, P. chirripoense, P. correae, P. cotonense* (rarely 2), *P. crassispathum, P. dressleri, P. dwyeri, P. edenudatum, P. folsomii, P. glanduliferum, P. granulare, P. hammelii, P. hederaceum, P. immixtum, P. jacquinii, P. jefense, P. knappiae, P. ligulatum* var. *heraclioanum, P. ligulatum* var. *ligulatum* (sometimes 2, rarely to 5), *P. ligulatum* var. *ovatum, P. madronense, P. mexicanum, P. microstictum, P. platypetiolatum* (rarely 2), *P. purpureoviride, P. purulhense, P. radiatum* var. *pseudoradiatum, P. squamipetiolatum, P. utleyanum, P. verapazense,* and *P. warszewiczii* (rarely to 3).

Most species with a single inflorescence per axil are either vines or appressed-climbing hemiepiphytes with internodes longer than broad.

The number of upper axils bearing inflorescences is also variable. Some species, e.g., *P. lentii,* rarely have more than one leaf axil bearing an inflorescence, while other species, e.g., *P. annulatum* and *P. fragrantissimum,* bear inflorescences in two or more of the closely spaced upper internodes, making it appear that the plants have a large number of inflorescences.

Species that regularly have up to four or more inflorescences per axil are: *P. copense* (to 6), *P. cotobrusense* (to 5), *P. clewellii* (to 6), *P. dodsonii* (2–5), *P. ferrugineum* (to 6), *P. fortunense, P. gigas* (to 7), *P. grayumii* (to 5), *P. heleniae* (to 10), *P. jodavisianum* (2–6), *P. panamense* (to 6), *P. pirrense, P. squamicaule* (to 5), *P. sousae, P. tenue, P. tysonii* (to 5), and *P. verrucosum.*

Species with five or more inflorescences per axil are rare, totaling only eleven. Only two species, *P. gigas* and *P. heleniae,* have up to seven inflorescences per axil.

PEDUNCLES

Typically the peduncle is terete but it may be somewhat flattened laterally, especially when there are clusters of inflorescences per axil. The peduncle is usually whitish or pale green at the base where it is often hidden by the leaf sheath. The remaining portion of the peduncle is usually dark to medium green with the surface often shortly pale-lineate like the petioles. The peduncle is often coarsely pale-ribbed near the apex, as in *P. copense, P. dodsonii,* and *P. findens.* Rarely is the peduncle pinkish red or reddish as in *P. malesevichiae, P. schottianum,* and *P. roseospathum* (or sometimes in *P. sulcicaule*) or tinged with red or purple as in *P. chiriquense, P. davidsonii* subsp. *bocatoranum, P. heleniae, P. grandipes, P. purpureoviride,* and *P. verrucosum.*

Most peduncles, like other parts of the average *Philodendron,* are glabrous, but some species have peduncles conspicuously covered with trichome-like glands, e.g., *P. squamicaule* (Fig. 384), *P. squamipetiolatum* (Fig. 388), and *P. verrucosum* (Fig. 440).

The peduncle is usually much narrower than the spathe, commonly no more that ⅓ to ¼ the width of the spathe tube, and is almost always broadened distally, merging almost imperceptibly with the spathe tube. Usually the color distinction is also gradual, but in some cases, e.g., *P. annulatum, P. dodsonii,* and *P. dolichophyllum,* there is an abrupt transition between the green peduncle and the colored spathe. In *P. ligulatum* there is a purple ring at the apex of the petiole, much like that at the apex of the petiole (Fig. 276).

The length of the peduncle, especially relative to the length of the spathe, may be important taxonomically. Some species, e.g., *P. antonioanum, P. crassispathum, P. davidsonii, P. ferrugineum, P. findens, P. malesevichiae, P. purulhense, P. radiatum, P. schottianum,* and *P. zhuanum,* have very short peduncles relative to the length of the spathe. In contrast, other taxa, e.g., *P. advena, P. angustilobum, P. dodsonii, P. hebetatum, P. heleniae, P. immixtum, P. mexicanum, P. pterotum, P. rothschuhianum,* and *P. wilburii* var. *wilburii,* have peduncles as long as or longer than the spathes.

Peduncles range in length from 1 to 25 cm, with

four taxa, *P. microstictum*, *P. pseudauriculatum*, *P. wilburii* var. *longipedunculatum*, and *P. verrucosum*, all having peduncles that attain the maximum length of 25 cm. Several additional species have peduncles that may be more than 20 cm long. These include *P. anisotomum*, *P. brunneicaule*, *P. panamense*, *P. pseudauriculatum*, *P. rothschuhianum*, and *P. scalarinerve*.

Many species of *P.* subg. *Philodendron* have peduncles more than 10 cm long. In addition to those mentioned above, 37 Central American species have peduncles more than 10 cm long, while 38 taxa (35 species) have peduncles less than 10 cm long. Sixteen species have petioles that may be less than 3 cm long, but only *P. knappiae* has a peduncle which does not exceed 3 cm in length.

SPATHES

The spathe of *P.* subg. *Philodendron* is highly variable in many regards. The spathe of *Philodendron* is typically coriaceous and constructed in such a way that the spathe may open and reclose without major alteration in its shape. The margins are invariably much thinner, with the apical portion of the spathe usually tightly rolled and frequently acuminate (Fig. 178, *P. findens*) and the basal portion more conspicuously convolute. Because the margins of the base are more conspicuously overlapped, when the spathe opens the lower portion remains convolute (Fig. 70, *P. auriculatum*) whereas the apical portion separates to very near the tip. Some species have spathes that open more fully so that the opening is almost rounded (Fig. 298, *P. panamense*) or broadly elliptic (Fig. 288, *P. mexicanum*). In such cases more of the inner tube surface and the pistillate portion of the spadix are exposed. On the other hand, some species have spathes that open only slightly so the opening is merely elliptic with the pistillate portion of spadix not visible without peering down through the top of the opening (Fig. 63, *P. antonioanum*).

Species vary greatly in the extent to which the spathe remains convolute at the base during anthesis. Spathes of some species, e.g., *P. angustilobum* (Fig. 51) and *P. mexicanum* (Fig. 288), unfold to very near the base. Those of other species, e.g., *P. antonioanum* (Fig. 63), do not open very broadly. The spathe tubes of *P. auriculatum* (Fig. 70), *P. panamense* (Fig. 298), and *P. wendlandii* (Fig. 451) remain convolute only in the lower half. The spathe of *P. davidsonii* (Figs. 134, 136) may be convolute only in the lower ⅓ to ⅗ in *P. squamicaule*. That of *P. hebetatum* (Fig. 226) is convolute to the upper ¼ and the spathe tubes of *P. aromaticum* (Fig. 68), *P. brenesii* (Fig. 89), *P. copense* (Fig. 110), *P. scalarinerve* (Fig. 140), *P. findens* (Fig. 177), *P. rothschuhianum* (Fig. 340), *P. straminicaule* (Fig. 360), and *P. schottianum* (Fig. 371) remain essentially closed to the apex of the tube during anthesis.

Mayo (1986) presented a classification of inflorescence types based principally on South American *Philodendron* species. Eleven inflorescence types were characterized, and a key was prepared to separate them. The characters chosen for use in the key were: (1) presence or absence of resin ducts in the inner surface of the spathe; (2) solitary vs. two or more inflorescences per axil; (3) relative length of the sterile staminate portion of the spadix (equal to or longer than the staminate portion vs. shorter than staminate zone); (4) presence or absence of colorful contrasts on inner surface of spathe tube; (5) prominently constricted vs. weakly constricted spathes; (6) presence or absence of resin ducts in the spathe; (7) presence of resin ducts in the sterile staminate portion of spadix vs. with resin ducts in either the fertile staminate portion or in both sterile and fertile staminate portions; (8) presence of non-functional resin canals in the spathe vs. resin canals lacking in the spathe (usually correlated with contrasting spathe colors); and (9) presence or absence of a terminal sterile zone on the spadix.

While I believe that this classification may be somewhat artificial, it demonstrates many evolutionarily important morphological features and shows the complexity of the *Philodendron* spathe.

Species of *P.* subg. *Philodendron* have the spathe tube relatively well demarcated from the blade either by being constricted at the apex or by its contrasting color. Some species, e.g., *P. crassispathum* (Fig. 124), lack any constriction above the tube, thus the spathe is more or less elliptic. Species that have a weakly constricted spathe include *P. advena* (Fig. 40), *P. alticola* (Fig. 45), *P. breedlovei* (Fig. 85), *P. purulhense* (Fig. 323), *P. schottianum* (Fig. 368), and *P. antonioanum* (Fig. 63). Despite these exceptions, most members of *P.* subg. *Philodendron* have spathes to some extent constricted. The subgenera *Meconostigma* and *Pteromischum*, on the other hand, have spathes not likely to be constricted or are only weakly constricted (Mayo, 1986).

Spathe length is relatively variable depending on the age of the plant and the stage of development. Elongation of the spathe is typically more or less arrested after anthesis, but sometimes a considerable amount of elongation takes place in both the peduncle and spathe after anthesis, presumably to accommodate the considerable expansion of the developing fruits. Spathe length varies from as little

as 4.5 cm in *P. clewellii* and 4.8 cm in *P. heleniae* to 29 cm in *P. pterotum* and 30 cm in *P. warszewiczii*. Relatively few species have spathes that ever exceed 25 cm in length even when in fruit.

Relatively few species have spathes less than 10 cm long. These are: *P. brewsterense, P. chirripoense, P. clewellii, P. dwyeri, P. knappiae, P. roseospathum* var. *angustilaminatum,* and *P. ubigantupense.*

The shape of the spathe and the relative disposition of the spadix at anthesis are taxonomically significant, but seldom described. This is because many species are still poorly known at anthesis, no doubt due to the fact that anthesis in *Philodendron* lasts only one or two days for each inflorescence.

One of the features that determines the shape of the spathe at anthesis is the degree to which the spathe opens. Spathes of some species, such as *P. aromaticum, P. copense, P. dodsonii, P. findens, P. fragrantissimum, P. grandipes, P. hebetatum, P. jodavisianum, P. straminicaule,* and *P. strictum,* open along the blade portion (see discussion above), leaving an oblong-elliptic opening (Fig. 110, *P. copense*; Fig. 140, *P. dodsonii*; Fig. 378, *P. smithii*). In these examples the spadix is either included within the spathe or is barely exserted, stiffly erect yet held slightly in front of the top edge of the spathe. On the other hand, spathes of some species, such as *P. angustilobum, P. mexicanum,* and *P. tripartitum* (Fig. 423), may open so broadly as to expose much of the pistillate portion of spadix. The pistillate portion of the spadix is usually for the most part obscured by the prominently convolute tubular portion of the spathe, as in *P. antonioanum, P. aromaticum, P. copense,* and *P. dodsonii.* Those species with spathes opening more broadly may also have the spadix protruding forward somewhat out of the spathe (see section on Spadix).

The definition of the spathe tube is somewhat imprecise, in terms of both morphology and color, but the spathe tube may be defined as the lower portion of the spathe (that portion which covers the pistillate portion of the spadix). In reality it usually extends somewhat above the pistillate portion to include the lowermost or sterile zone of the staminate portion of the spadix. In cases where the spathe has an obvious constriction it is that portion below the constriction (the balance being the spathe blade) that is referred to as the spathe tube. Though the ending of the spathe tube is imprecise, it generally terminates where the greatest constriction of the staminate portion of the spadix occurs, usually immediately above the sterile staminate portion of the spadix. Functionally, the constriction of the spathe, coinciding with the narrowest portion of the staminate portion of the spadix, prevents much of the pollen from the fertile upper portion of the spadix from falling directly into the chamber of the pistillate portion of the spathe. This probably serves more to prevent wastage of the pollen (by containing the pollen in a place where it can most easily be carried away by beetles) than it does to prevent self-pollination, since most species are so markedly protogynous that no self-pollination is possible, i.e., the pistils are probably no longer receptive when the pollen is shed. Testing for pistil receptivity with the use of peroxidase paper, Grayum (1996) found stigmas receptive throughout the period of staminal dehiscence in *P.* subg. *Pteromischum,* but numerous attempts at self-pollinations of members of *P.* subg. *Philodendron* by me and others failed to produce berries and instead resulted in aborted inflorescences. Not surprisingly those species, e.g., *P. advena, P. crassispathum* (Fig. 124), and *P. purulhense,* that have spathes scarcely constricted above the tube also have spadices not markedly narrowed above the sterile staminate flowers. It is not known whether the pollination behaviors of these species differ.

For *Philodendron* species with a prominent spathe constriction, the partially closed spathe during staminal anthesis, coupled with the swollen area of the staminate portion of the spadix immediately below it, provides a "pollen well" through which the beetles must squeeze on their departure. This probably ensures a greater coverage of pollen for the departing beetle pollinators.

Spathe tube shape and length are not particularly useful taxonomically. Tubes range in shape from virtually oblong (e.g., in *P. heleniae, P. ligulatum,* and *P. tripartitum*), to oblong-elliptic (e.g., in *P. aromaticum, P. copense, P. dodsonii, P. findens, P. gigas, P. hebetatum,* and *P. pseudauriculatum*) to elliptic (e.g., *P. rothschuhianum* and *P. smithii*), and range from only 2 cm long in *P. clewellii* to 14 cm long in *P. davidsonii* and *P. warszewiczii.* Species with spathe tubes longer than 10 cm are: *P. auriculatum, P. ferrugineum, P. schottianum, P. sousae,* and *P. tysonii.* Seventeen species have spathe tubes less than 5 cm long.

Even though the spathe tube often remains totally closed at anthesis it is, nonetheless, still somewhat expanded owing to the separation caused by the flaring of the spathe blade. Generally this provides considerable room around the spadix to accommodate the pollinating beetles (Figs. 100, 128, 242, 268). At anthesis the spathe tube is considerably more voluminous than before anthesis.

Spathe color. Spathe coloration is generally taxonomically significant though variable depending on

the age of the inflorescence. Before anthesis spathes are frequently green on the outside, but reddish coloration often develops well in advance of anthesis. Coloration of the spathe tube and blade often differs, with the spathe tube more commonly various shades of green and the spathe blade more commonly white, whitish, or whitish green. Even when the spathe is green throughout, the spathe blade is typically paler green than the tube. The tube portion of the spathe is commonly colored or tinged with red, maroon, or purplish violet (sometimes with other shades of red, orange, or purple) on one or both surfaces. Strong color contrasts (other than merely green vs. white), so common in *Philodendron*, are absent in other ostensibly related genera, namely *Furtadoa*, *Homalomena*, and *Anubias* (based on the *Philodendron* Alliance of Mayo, Bogner & Boyce, 1995) and also *Cercestis* and *Culcasia* (included in the *Philodendron* Alliance of Grayum, 1990). This would also be true of other presumed relatives including *Dieffenbachia*, *Montrichardia*, *Nephthytis*, *Peltandra*, *Typhonodorum*, and even *Zantedeschia*.

Generally if the spathe is colored on the outer surface it is also colored on the inner surface (but the reverse is not true). The inner surface is typically much more intensely colored than the outer surface. The coloration of the inner surface of the spathe, though commonly more or less restricted to the tube, may extend well onto the blade, sometimes even to very near the apex, such as in *P. breedlovei*, *P. davidsonii*, *P. mexicanum*, and sometimes *P. sagittifolium*. In some cases, such as *P. findens* and *P. schottianum*, the color is merely weakly diffused onto the inside of the blade. At other times only the very base of the tube is colored inside, such as in *P. ligulatum* and *P. hederaceum*. The spathe blade is commonly more extensively colored on the outer than on the inner surface, although blade coloration is highly variable, both inter- and intraspecifically. Nevertheless, most species have spathe blades some shade of green or white on the outer surface, often tinged with red, pink, purple, or yellow. A few species, such as *P. sagittifolium* and *P. ferrugineum* (Fig. 167), have purplish spots or blotches throughout much of the exterior of the spathe surface. Although the external coloration of the spathe is usually restricted to the tube portion, it often extends onto the blade, a situation that happens more frequently on the outer surface of the spathe than on the inner surface. Species that have coloration extending well above the spathe tube are: *P. antonioanum*, *P. breedlovei*, *P. dolichophyllum*, *P. subincisum*, and *P. roseospathum*. Sometimes the coloration of the spathe may be restricted to the tube, but only near the margins of the open edge such as in *P. grayumii* and *P. malesevichiae*.

While some species, e.g., *P. alticola*, *P. heleniae*, and *P. findens*, show little or no distinction in the coloration of the spathe tube and spathe blade, other species have distinctly different colors. In some cases, e.g., *P. antonioanum*, *P. cretosum*, *P. edenudatum*, *P. findens*, *P. grandipes*, *P. lazorii*, *P. ligulatum*, *P. llanense*, and *P. roseospathum*, the transition from one color to the next is very gradual. In other cases, such as *P. hebetatum*, *P. immixtum*, *P. jodavisianum*, *P. panamense*, *P. pterotum*, *P. strictum*, *P. radiatum*, *P. rothschuhianum*, *P. scalarinerve*, *P. smithii*, *P. tenue*, *P. wendlandii*, and *P. zhuanum*, the transition is less gradual but by no means abrupt. Still other species, e.g., *P. ligulatum* var. *ovatum*, *P. dodsonii*, *P. gigas*, *P. strictum*, and *P. fragrantissimum*, show a distinct and abrupt transition in the spathe tube and blade colors.

The biological significance of the frequently darker colors on the inside of the spathe tube in contrast to the paler colors of the spathe blade is uncertain. It seems unlikely that either the contrasting colors or the dark color of the spathe tube act in attracting pollinators. The presumed pollinators, dynastine scarab beetles (see section on "Pollination Biology"), are believed to orient more by smell than sight (Faegri & van der Pijl, 1979; Gottsberger & Silberbauer-Gottsberger, 1991). Moreover, their normal arrival time, near dark, would probably preclude their seeing contrasting colors in any event. In addition, the dark coloration is usually restricted to the spathe tube and often not even visible in good light from near the mouth of an open spathe. It is more likely that the dark-colored spathe tube acts to encourage these crepuscular beetles to stay for an extended period of time. Mayo (1986) pointed out that, since neither *P.* subg. *Pteromischum* nor *P.* sect. *Meconostigma* have color contrasts in the spathe blade and tube, *P.* subg. *Philodendron* may have different pollinators. Although not enough pollinators have yet been identified to confirm this possibility, there seems to be little evidence in favor of Mayo's hypothesis (see section on "Pollination Biology"). Some beetle species, such as *Erioscelis proba* Sharp, are known to visit species of both *P.* subg. *Philodendron* and *P.* subg. *Pteromischum* (Grayum, 1996) (see also Table 3, "Pollinators of *P.* subg. *Philodendron*").

Lenticel-like structures on both the exterior of the spathe tube and the peduncle in some *Philodendron* species secrete large droplets of a viscous, somewhat sweet substance. Mayo (1986) has shown that these may consist of clusters of stomata, and

Table 3. Pollinators of *Philodendron* subg. *Philodendron*.

Plant species	Voucher	Beetle species
P. anisotomum		**Cyclocephala amblyopsis* Bates
		**Erioscelis columbica* Endrödi
P. brenesii	*Croat 35519*	*Cyclocephala nigerrima* Bates
P. brevispathum		*Erioscelis proba* Sharp
P. callosum	No voucher	*Cyclocephala rustica* (Olivier)
P. correae	*Croat 66653*	*Cyclocephala conspicua* Sharp
P. grandipes	*Croat 76594*	**Cyclocephala gravis* Bates
	Jiménez 6	*Cyclocephala sexpunctata* Castelnau
	Jiménez 6	*Erioscelis columbica* Endrödi
	Croat 43289	
P. grayumii	*Croat 74840*	*Cyclocephala rubescens* Bates
	Croat 74840	*Cyclocephala sexpunctata* Castelnau
P. jodavisianum	*Croat 35950*	*Cyclocephala ligyrina* Bates
	Croat 35950	*Cyclocephala mafaffa* Burmeister
		**Erioscelis columbica* Endrödi
P. ptarianum	*Ramírez 1163*	*Cyclocephala rustica* (Olivier)
P. pterotum		**Cyclocephala ampliata* Bates
		**Cyclocephala amblyopsis* Bates
	Croat 10903	*Cyclocephala ligyrina* Bates
		**Cyclocephala sexpunctata* Castelnau
P. radiatum		**Cyclocephala ampliata* Bates
		**Erioscelis columbica* Endrödi
		**Cyclocephala amblyopsis* Bates
		Cyclocephala ligyrina Bates
		Cyclocephala kaszabi Endrödi
P. rothschuhianum		**Cyclocephala amblyopsis* Bates
	(Young, 1987)	*Cyclocephala kaszabi* Endrödi
		**Erioscelis columbica* Endrödi
P. sagittifolium	*Thompson 4636*	*Cyclocephala sexpunctata* Castelnau
P. schottianum	*Croat 36110*	*Cyclocephala melane* Bates
P. tripartitum		**Cyclocephala amblyopsis* Bates
		**Cyclocephala kaszabi* Endrödi
		**Erioscelis columbica* Endrödi
P. tysonii	*Croat 66711*	*Cyclocephala nigerrima* Bates

*Entries were provided by Helen Young, Barnard College, New York, and were based on unpublished observations made during 1984–1985 at La Selva (O.T.S. Field Station) in Costa Rica (with the assistance of George Schatz). Entries without an asterisk were based on determinations made by John Rawlins at Carnegie Museum in Pittsburgh. Collections by S. Thompson were contributed independently to Rawlins.

pointed out their possible ecological significance as extrafloral nectaries.

The secretion of resin from the inner surface of the spathe is apparently unique, in Araceae, to *Philodendron* (Mayo, 1991). Mayo (1986) enumerated four different types of inflorescence resin canals, at least two of which occur among Central American *Philodendron*. One type, found in *P. tripartitum*, has large-diameter resin canals imbedded just beneath the epidermis on the inner surface of the spathe. Resin is secreted directly onto the surface. Another type, represented by *P. smithii*, lacks resin canals on the spathe but instead has resin canals in the staminate zone of the spadix.

The two other types of resin canals pertain to *P.* subg. *Meconostigma* and *P.* subg. *Pteromischum*. In the former, exemplified by *P. bipinnatifidum* Schott ex Endl., the resin canals are "J"-shaped and tangential, arising in the aerenchyma of the spathe and extending to the surface. In the latter, exemplified by *P. sonderianum* Schott, the resin canals are evenly distributed between the aerenchyma and epidermis and are parallel to the surface of the epidermis rather than arising in a J-shaped fashion.

Resin canals usually are present in the proximal ½ to ⅔ of the spathe blade and sometimes also the distil portion of the tube. In *P.* subg. *Philodendron*, these resin canals are generally reddish, red-pur-

ple, or orange to brownish and generally somewhat intermittent, as in *P. sulcicaule*, though sometimes continuous, as in *P. immixtum*, *P. mexicanum*, *P. sagittifolium*, and *P. wilburii*. They are always oriented vertically, paralleling the veins of the spathe. The resin canals actively secrete a resinous liquid at anthesis that wells up onto the surface of the spathe and sometimes runs down the spathe below the resin ducts. The resin is generally very sticky and probably functions in causing pollen, sometimes itself not particularly sticky, to adhere to the bodies of the beetle pollinators as they leave the spathe.

SPADIX

Philodendron species are monoecious, with the spadix bearing naked unisexual flowers. The flowers lack a perigon and are closely arranged on a more or less cylindrical spadix, with the staminate flowers comprising the upper ⅖–⅘ of the spadix and the pistillate flowers comprising the remaining basal portion. The average spadix for *P.* subg. *Philodendron* in Central America has the staminate portion 2.2 times longer than the pistillate.

The spadix is usually contained for the most part inside the spathe at anthesis (see section above on the Spathe), although in the majority of species the spadix is weakly exserted in front of the spathe. The majority of plants at anthesis have their spathes erect or tipped slightly forward so they can provide shelter to spadices from water dripping straight overhead.

Spadices of some species, especially those with broadly opened spathes (e.g., *P. angustilobum* (Fig. 51), *P. ligulatum* (Fig. 266), *P. mexicanum*, and *P. tripartitum*) protrude prominently forward at anthesis. Other species whose spathes remain convolute to about the middle may also have spadices that protrude prominently forward; these are: *P. auriculatum*, *P. davidsonii*, *P. grayumii*, *P. hebetatum*, *P. heleniae* (Fig. 229), *P. jodavisianum*, *P. ligulatum*, *P. llanense* (Fig. 268), and *P. panamense* (Fig. 299).

The spadix of *Philodendron* is usually only slightly shorter than the spathe. The average length of the spathe is 16.5 cm, while the average spadix is 15.8 cm long. Thus on average, the spathe is nearly 1 cm longer than the spadix. This difference may be as little as a few millimeters or as much as 4 cm.

The general morphology of the spadix of *Philodendron*, though highly variable in detail, is more or less the same for all species in Central America. The pistillate portion is usually pale green to greenish white and obliquely attached to the spathe, and sometimes markedly stipitate at the base. The floriferous part of the spadix is thus longer on the adaxial (front) than on the abaxial (back) surface (Fig. 40). The differences in the length of the adaxial and abaxial surfaces of the pistillate portion of the spadix depend on the angle at which it is attached to the spathe. These are referred to as "front side" and "back side" of the spadix in the descriptions presented in this revision.

The staminate portion of the spadix characteristically has a swollen sterile section at the base. Typically the staminate portion is broadest at the sterile section and gradually constricted just above this. Above the constriction the spadix is fertile and is gradually broadened usually to a point about ⅔ of its length, then narrowed gradually or abruptly to the tip.

The staminate portion is usually uniformly white to creamy white on the outside, although sometimes with the axis pinkish. Immature spadices are usually green, though they become white well before anthesis. The sterile section of the staminate portion is commonly a different color than the fertile section. Often it is more nearly white at an earlier stage of development when the fertile flowers are typically green. At anthesis the sterile staminate portion is more likely to be tinged with yellow or tan, reflecting the higher concentration of oil in these flowers than in the fertile flowers (see below). However, sometimes at anthesis the sterile and the fertile staminate flowers are identical in color. The sterile staminate portion frequently can be distinguished easily after anthesis with the sterile portion maintaining a white color (Fig. 28) while the fertile portion turns grayish or brownish. The sterile staminate portion can usually be distinguished even in these cases by the difference in the size of the spadix (usually larger than the adjacent fertile staminate portion), by the usually larger and more irregularly shaped flowers, and because the sterile staminate section typically ends just before the narrowly constricted portion of the fertile staminate portion (which itself coincides with the constricted portion of the spathe). The sterile staminate flowers are often more easily discernible on dried specimens than they are on live ones since they tend to dry a different color, usually somewhat more brownish.

The much higher oil content of the sterile staminate flowers was reported by Pohl (1932), and it is probably owing to this high oil content that the sterile staminate flowers are often eaten by the beetle pollinators (Fig. 29). A high concentration of

lipids in the mitochondria of the staminodial cells has been documented (Walker et al., 1983).

The fertile staminate portion of the spadix is typically more or less clavate and bluntly tapered toward the apex. In a few species, such as *P. advena, P. crassispathum,* and *P. davidsonii,* it is more nearly oblong-ellipsoid, often broadest at the base and bluntly tapered toward the apex. The spadix of *P. ferrugineum* is similarly shaped but is somewhat more constricted above the sterile staminate portion. Some species, e.g., *P. heleniae,* have the spadix broadest in the upper ⅓ rather than in the sterile staminate portion.

Male flowers. The androecium of *P.* subg. *Philodendron* is truncate at the apex, prismatic to obpyramidal and usually irregularly 4–5-sided (Fig. 30). It consists of 2–6 sessile stamens (mostly 3–4). These are always distinct for most of their length although often weakly fused at the base. Stamen number varies within a single spadix and is never constant (Mayo, 1986). Despite the clear grouping of stamens it is sometimes difficult to discern clear floral groupings, especially when the stamens are distinct. Mayo (1986) reported that some species have stamens dehiscent laterally rather than extrorsely.

The androecia in *P.* subg. *Philodendron* range from 2 to 6 mm diam. and show little interspecific variation. Stamens of all species studied by Mayo (1986) had druses in their apices. Anthers are sessile to subsessile with a thick connective that is truncate at the apex and overtops the thecae. The connective of all species studied by Mayo (1986) had raphides present. The thecae are ellipsoid, oblong or linear, emarginate at the base, and each opens by a short lateral slit or subapical pore. The two thecae of a stamen are generally adjacent in *P.* subg. *Philodendron* but positioned far apart in *P.* subg. *Pteromischum* and *P.* subg. *Meconostigma.* Anther thecae lack cell wall thickenings in the endothecium in *P.* subg. *Philodendron* (French, 1985).

Pollen typically emerges in long, slender, somewhat viscid filamentous strands (Fig. 31) (see section on "Pollination" for a description of its emergence). These slender strands of pollen do not persist for many hours, and ultimately the pollen becomes matted in irregular clusters (Fig. 391, *P. straminicaule*).

In *P.* subg. *Philodendron* resin canals in the staminate portion of the spadix are situated beneath the stamens and secrete resin onto the surface of the stamens. The same is not true of *P.* subg. *Pteromischum* and *P.* sect. *Meconostigma,* where the resin canals are borne at a deeper level in the axis and do not secrete resin onto the surface of the stamens (Mayo, 1986) (Fig. 128, *P. crassispathum*).

French (1986a) reported that the stamen vasculature of most species of *P.* subg. *Philodendron* consists of a single forked bundle with widely divergent branches. Carvell (1989) reported that a single unbranched trace supplies each stamen. According to Mayo (1986) the staminodia have a more distinctive floral receptacle than do the fertile staminate flowers and often have a multiple-branched vascular trace, whereas the latter have an indistinct floral envelope and only a once-branched vascular trace. In contrast, members of *P.* subg. *Meconostigma* have traces that lack branches or have only short branches that spread at an acute angle.

Stamens in *P.* subg. *Philodendron* have both druses and raphide idioblasts with secondarily thickened walls and tanniniferous idioblasts occurring throughout the ground tissue (Carvell, 1989).

POLLEN

Anthers of *Philodendron* (Grayum, 1991) have a two- or more-layer tapetum of a periplasmodial type. Pollen mother cell cytokinesis is probably successive.

Philodendron pollen (Fig. 30) is binucleate (Zavada, 1983; Grayum, 1985, 1986, 1992a), inaperturate, starchy and of moderately large size (averaging 40 µm, ranging 28 µm–40 µm), with subisopolar polarity (Grayum, 1985, 1991). As in most aroid genera, it is shed in monads. Pollen is typically boat-shaped-elliptic to oblong, or occasionally elongate as in *P. radiatum.* It is usually round in cross section, but may be very obscurely keeled in *P. hederaceum* to moderately keeled in *P. jacquinii, P. jodavisianum,* and *P. wendlandii,* or prominently keeled in *P. mexicanum.* The exine sculpturing is usually psilate, but sometimes minutely verruculate, scabrate, or fossulate (*P. fragrantissimum, P. grandipes, P. jacquinii, P. jodavisianum,* and *P. pterotum*) to punctate, subfossulate, subfoveate, or subverrucate (*P. mexicanum* and *P. wendlandii*).

FEMALE FLOWERS

The pistils of *P.* subg. *Philodendron* are closely aggregated on the spadix in a series of irregular spirals. Gynoecial characters have long been considered important in the subgeneric classification of *Philodendron,* and lobed stigmas were used as early as 1832 by Schott in the recognition of his greges *Meconostigma* and *Sphincterostigma* (the latter now a synonym of the former). The number of

ovules per locule was used by Engler (1878) in part to characterize the two largest sections of the genus, *Oligospermum* Engl. and *Polyspermium* (now *Calostigma* and *Philodendron*, respectively) (Mayo, 1990).

The pistillate flowers consist of a single naked pistil lacking staminodia. Typically the ovaries are ovoid to obovoid or elliptic, and terete in cross section, or with the sides often somewhat irregularly angular by compression owing to their close proximity with adjacent pistils. Embryo sac development is of the *Polygonum*-type (Grayum, 1991). Each ovary for the genus is syncarpous, superior, and contains 2–47 locules (4–10 in *P.* subg. *Philodendron* of Central America). Ovaries range in size from 0.5 mm (as in *P. sousae*) to 9.2 mm long (as in *P. advena*). The locules are typically oblong, with thin translucent walls that extend ⅖–¾ the length of the ovary. The style is barely distinguishable from the remainder of the ovary, mostly by being slightly thicker and opaque, rather than translucent. While Dahlgren and Clifford (Dahlgren et al., 1985) reported no style in Araceae, both Eyde et al. (1967) and Mayo (1986, 1989) indicated that the region has a distinct anatomy. Mayo (1989) defined the style of *Philodendron* as "that portion of the gynoecium between the base of the stigmatic epidermis and the ovary locules." Slender, conspicuous styles are rare in *Philodendron*, but do exist, as in *P. jacquinii* (Fig. 242).

Each carpel is connected to the stigma apex or compitum (common stylar canal) by a stylar canal. The compitum (Endress, 1982) is a cavity or complexly shaped channel into which the pollen may be inadvertently packed by the beetle pollinators. This no doubt allows for enough grains to be left to insure pollination, and to make sure not all are removed from the stigma by movements of the beetles. The stigmatic epidermis extends into the compitum from the stigma apex (Mayo, 1989). At the base of the channel or cavity there is a ring of holes that leads into the stylar canals. Where no compitum is present, such as with "Type B" and "Type D" styles (see section on "Style Types" below), the stylar canals lead directly onto the surface of the style. These canals are readily visible on the dried stigmas of many species if the preservation is adequate. They are particularly easy to see in fruiting collections.

The gynoecium has a separate stylar canal for each carpel (see fig. 1 in Mayo, 1989). Each canal may open at its upper end into a compitum. A compitum is rare among Central American species (see section on Style Types below), but is present in *P. correae*, *P. ligulatum* var. *heraclioanum*, *P. smithii*, *P. straminicaule*, and *P. warszewiczii*. A compitum has also been seen on an unusual collection of *P. radiatum* and some populations of *P. tripartitum*.

The vascular anatomy of *Philodendron* ovules has been studied by French (1986b). Of the five species he studied, three were South American while two, *P. jacquinii* ("*P. hederaceum*") and *P. inconcinnum* ("*P. immixtum*"), occur in Central America. French reported a single vascular trace for all of these except *P. jacquinii*, which has multiple traces. Carvell (1989) reported that the vasculature of the gynoecium in *Philodendron* arises from a single trace, which divides centrifugally to yield a single branch trace for each locule. The carpel traces branch once to form a connection with the placenta as well as a single dorsal trace. The placental trace forms individual connections with each ovule (Carvell, 1989).

Finally, a few miscellaneous anatomical features of the gynoecium should be mentioned. Both tanniniferous idioblasts as well as raphide idioblasts are lacking in the gynoecium of *Philodendron*, but the gynoecium does contain druse idioblasts (Carvell, 1989). Like most Araceae, *Philodendron* has unicellular ovular and placental trichomes (French, 1987b). These function in secreting mucilage presumably for the protection of ovules.

Ovules of *Philodendron* are bitegmic, with the inner integument forming the micropyle. The integuments are usually completely free from one another (Grayum, 1991).

Seemingly the most important morphological features of the pistil from the standpoint of systematic importance are the quantity and distribution of the ovules and the type of style, discussed in subsequent sections.

Placentation. Placentation type for *P.* subg. *Philodendron* in Central America is usually axile or sub-basal, with 50 species having sub-basal placentation and five species with basal placentation. Those with basal placentation are: *P. dwyeri*, *P. granulare*, *P. smithii* (also sometimes sub-basal), *P. sousae* (also sometimes sub-basal), and *P. zhuanum*. Forty-seven species have axile placentation and two additional species, *P. ferrugineum* and *P. sagittifolium*, with mostly sub-basal placentation, sometimes have axile placentation when they have especially numerous ovules per locule.

Some general rules regarding placentation type and number of ovules per locule are the following: species with basal placentation have only a solitary ovule per locule and tend to have a few large seeds per berry. Species with sub-basal placentation usually have only 1 to a few ovules per locule (aver-

aging 2.1 to 3.5 respectively for the minimum and maximum number in the range) and typically fewer than 6 but rarely to 10 or to 12 (as in *P. brenesii* and *P. davidsonii* subsp. *bocatoranum*). Species with basal and sub-basal ovules tend to have rather large seeds as well, although sometimes their seeds are quite small. On the other hand, species with axile placentation usually have 10 or more ovules per locule (averaging 14–18 respectively for the minimum and maximum in the range) but sometimes as few as 3 (*P. dressleri* and *P. warszewiczii*), or 4.

For those species with only a few ovules per locule, the disposition of the ovules seems to be unorganized or digitate, but for those with more than a few ovules, the placentas may be uniseriate or more generally biseriate or, less frequently, in 1–2 or 2–3 series (see Appendix 2, "Technical Data on Pistils"). Mayo (1989) reported that, based on his studies of the gyneocial morphology and anatomy of 15 mostly South American *Philodendron* species, the placenta of even those species whose ovules appear to be in a single row might actually be biseriate, with the funicles inserted alternately along the placental ridge. This is also true in Central American species. Forty Central American taxa of *Philodendron* proved to have biseriate placentas, while much smaller numbers appeared uniseriate (13), 1–2-seriate (9), 2–3-seriate (11), or digitate (4). Twenty-six species lacked any appreciable organization owing to the small number of ovules, and one species, *P. niqueanum*, was not studied due to inadequate material.

Ovary locule number. Mayo (1991) reported that ovaries in *P.* subg. *Meconostigma* range from 3- to 47-locular, and Bunting (1986) reported 2 (rarely 3) locules per ovary as characteristic of *P.* sect. *Philopsammos*.

Though the number of ovules per ovary is highly significant in separating *P.* sect. *Philodendron* and *P.* sect. *Calostigma*, the number of locules is not a good indicator of relationship. While the average number of locules per ovary has a slightly lower range for *P.* sect. *Philodendron* (4.6–6.1 vs. 5.5–7.4 for *P.* sect. *Calostigma*), the difference is not great. In *P.* sect. *Calostigma* the number of locules per ovary ranges from 1 to 10. In *P.* sect. *Philodendron* it ranges from 3 to 10. While *P.* sect. *Philodendron* rarely has more than 8 locules per ovary, and *P.* sect. *Calostigma* rarely has fewer than 5, more species (14 in all) have 8 locules per ovary than any other number.

No species of *P.* subg. *Philodendron* in Central America were found to have bilocular ovaries, though two species, *P. sagittifolium* and *P. zhuanum*, may have only a single locule. In the latter species, the number of locules ranged only from 1 to 3, but in *P. sagittifolium* the number of locules ranged up to 8. Often such low locule numbers occur only near the base of the spadix, where the ovaries are often somewhat irregular in shape. Frequently, the lowermost pistils on the spadix are larger or smaller than those in the middle of the spadix and are more widely spaced and of irregular cross-sectional shape. Three-locular ovaries are rare, known only in two species: *P. copense* and *P. sagittifolium*. Five other species, *P. chirripoense*, *P. hederaceum*, *P. immixtum*, *P. morii*, and *P. squamicaule*, may rarely have 3-locular ovaries.

Four-celled ovaries are fairly common in *P.* subg. *Philodendron*. Four species, *P. cretosum*, *P. jacquinii*, *P. knappiae*, and *P. subincisum*, so far have demonstrated only 4-locular ovaries. Most species with 4-locular ovaries also have 5-locular ovaries on the same spadix. Four species showed exclusively 5-locular ovaries. Only eight species have locule numbers greater than 10; all but one of these are in *P.* sect. *Calostigma*.

Ovules per locule. The number of ovules in each locule varies from 1 to numerous. Mayo reported numbers as high as 51 for *P.* subg. *Meconostigma*, but my studies of *P.* subg. *Philodendron* show the highest number found for any Central American species is 36, in *P. fragrantissimum*. Only 4 other species, *P. antonioanum*, *P. panamense*, *P. squamipetiolatum*, and *P. verrucosum*, have 30 or more ovules per locule, and 17 species have 20–29 (see Appendix 2, "Technical Data on Pistils"). Fifty-six species (62 taxa) have fewer than 10 ovules per locule.

Along with leaf morphology, the number of ovules per locule has long been used as a principal means of assigning sectional affinity in *Philodendron* (Engler, 1878, 1879, 1899; Krause, 1913; Mayo, 1989). Central American members of *P.* subg. *Philodendron* generally fall into three categories in terms of number of ovules per locule. Many species, including most members of *P.* sect. *Calostigma*, *P.* sect. *Tritomophyllum* and *P.* sect. *Baursia*, have one to few (rarely to 4 or 5, but always with basal or sub-basal placentation). Forty-four species and four subspecies belong to this category. A second group, with axile or sub-basal placentation, generally has 4–10 ovules per locule, but sometimes up to 14. Nineteen species fall into this category. The third group has exclusively axile placentation, mostly with many (15+) ovules per locule. These groups may not be natural, since two

species (*P. davidsonii* and *P. roseospathum*) have one variety in each of the aforementioned groups.

It might be expected that, since the pistils of different species of *Philodendron* are roughly the same size (mostly ranging from 1 to 4 mm long and about ½ to ⅓ as wide), the size of the ovules might be larger in those species with fewer ovules per locule than in those with more. Though there are differences in ovule size (see Appendix 2, "Technical Data on Pistils"), they are not great. Of 44 species of *Philodendron* studied that had axile placentation, the ovules ranged from 0.1 to 2.1 mm long. Alternatively, 48 species with basal or sub-basal placentation had only slightly larger ovules, ranging from 0.31 to 0.5 mm long.

Ovules in *Philodendron* are hemiorthotropous or orthotropous (Grayum, 1991), rarely hemianatropous (Mayo et al., 1997) and bilaterally symmetrical with an eccentric attachment of the funiculus (French, 1986b). The funicles are usually as long as or longer than the ovules. The ovules that are axile usually have funicles of different lengths, since they are positioned increasingly higher on the axis. After meeting with the wall of the locule the funicle is lightly fused to the wall all the way to the base and can be easily removed intact by pulling it free. This might argue against the assumption by Mayo (1989) that basal and sub-basal placentation were derived from axile placentation, since axile placentation could have developed by a lengthening of the funicular plexus and a fusion to the wall. While no anatomical study was made of this phenomenon, the frequent presence of basal funicles in axile placentas makes it appear that at least in the case of some Central American species of *P.* subg. *Philodendron*, species with axile placentation may have evolved from species with basal or sub-basal placentas.

The funicles in *P.* subg. *Philodendron* are frequently densely covered with short, usually inconspicuous, gland-like trichomes from near the base, sometimes extending to about half their total length. The secretory trichomes are continuous with those of the placentas and lining of the stylar canals (Mayo, 1989).

Funicles often bear a band of glandular trichomes at or near the base. These were well illustrated by Krause (1913) who reported them commonly in *P.* sect. *Baursia* and *P.* sect. *Calostigma* but with a few in *P.* sect. *Philodendron* as well. These small glands can only be seen under high magnification and probably secrete mucous into the ovary, preventing the ovules from drying out.

Funicles are often fused into a thickened, sometimes ramified, more or less translucent placenta. The entire placenta and its associated funicles and ovules may be removed, making counting them less difficult. Sometimes, however, adjacent locules share a common trunk so that care must be taken to insure that one is not removing the contents of two locules.

The free portion of the funicle on species with axil placentation seems to be proportionately shorter than the free portion of those with sub-basal placentation. This is perhaps because those species with axile placentation have somewhat longer locules allowing greater spacing of the ovules. Those species with sub-basal placentation and three or more ovules per locule have the funicles arising from one small area near the base of the axile wall, and often have much smaller locules than those with axile placentation. Ovules need to be separated for proper development, and funicles of different lengths allow for this. Thus, in many cases, funicles are longer in those species with sub-basal placentation. The generally smaller locule size for species with sub-basal or basal placentation is confirmed by a survey of locule size. Species with basal or sub-basal placentation have locules ranging in length from 0.32 mm in *P. jefense* to 9.5 mm in *P. warszewiczii*, with the average minimum length 1.9 mm and the average maximum length 3.5 mm. On the other hand, locules range in length from 0.40 (*P. bakeri, P. sousae, P. sulcicaule,* and *P. wilburii* var. *longipedunculatum*) to 0.7 mm (*P. advena*); the average minimum length is 1.12 mm while the average maximum is 1.75 mm.

The funicles of a single ovary are usually not of equal length if the ovules are basal or sub-basal, since the ovules are usually positioned at slightly different heights off the floor of the locule. Even when the ovules are scattered along much of the length of the axis of the locule wall, the funicles are of slightly different sizes.

Style and stigma morphology. This treatment follows the classification of styles and stigmas of Mayo (1989). Mayo (1986) defined the style in *Philodendron* as "that portion of the gynoecium between the ovary locules and the base of the stigmatic epidermis." Although there is considerable diversity at the microscopic level, much of the detail of the style is easily visible only by dissection (see section entitled "Style Types"). The fresh styles of *P.* subg. *Philodendron* are relatively uniform microscopically. Usually they are hemispherical or sometimes globose or depressed-globose. The microscopically visible portion is the stigma, a "single continuous area in which the epidermal cells are greatly elongated into secretory papillae" (Mayo, 1986). This

dense layer of stigmatic papillae is so closely packed and so engulfed in a gelatinous fluid as to appear almost solid. Still, a needle can be passed easily across and through much of its volume in any direction without disturbing its shape. The stigmatic papillae are slender, many times longer than broad, and attached to the surface of the style. Mayo (1986) reported that the stigmatic papillae often contain tannin cells.

The stigmatic papillae typically dry to form a thin, flat, often translucent, wafer-like mantle around the now somewhat visible style apex. In time the stigmatic mantle may fall off altogether allowing easy inspection of the style apex. Sometimes the stigma dries erect and disheveled. In these cases the appearance of the stigmas is more difficult to determine but, regardless of how the stigma dries, the style apex often can be made easily visible on a dried specimen by lightly scraping away the stigmatic papillae. The complexities of the style types of *Philodendron* are discussed below.

Style types. The present work adopts the gynoecial classification of Mayo (1989) in which six distinct style types were described and illustrated (Fig. 469, "Style Types in Central America"; see Appendix 2, "Technical Data on Pistils," which summarizes the style types for *P.* subg. *Philodendron* of Central America). Only two species, *P. niqueanum* and *P. utleyanum,* have style types not yet known. The table also includes the number of locules per ovary, placentation type, number of ovules per locule, ovary size, disposition of ovary, and the nature of the ovular sac when present.

Style type is one of the most important gynoecial features in *Philodendron.* While the stigma is moderately uniform in its superficial appearance, the style is highly diverse in morphological features. Unfortunately, these features are largely hidden by the stigmatic papillae when the pistil is fresh. Despite the shape of the style, the stigmatic papillae, which cover all or part of the style, may form a stigma of more or less uniform shape.

Style Type A has a compitum (common funnel into which the pollen may be packed, defined as the space between the upper stigmatic papillae and the level at which the stylar canals emerge onto the style surface) with ridged inner walls and a lobed apex, with each lobe corresponding to the apex of one carpel. Style Type A is restricted to *P.* subg. *Meconostigma* and thus will not be considered further here.

Style Type B (Fig. 469A) lacks a compitum. Instead, the stylar canals open into relatively broad concavities on the style apex. These concavities are arranged in a ring with one hole per locule. Style Type B also has the stylar canal entering directly into the apex of the locular cavity. Although the style apex may be completely flattened or broadly concave, it is sometimes weakly ridged between the apertures of the stylar canals. These ridges meet in the middle of the style and may even form a weak central beak. Some styles also have well-developed stigmatic papillae associated with the stylar canals causing the surface to be at least weakly lobed, with a single lobe for each locule. In dried condition Style Type B sometimes appears as a button-like structure, somewhat resembling Style Type D. It is therefore important in determining style type to make comparisons of material at or near anthesis. Style Type B seems to be most closely related to Style Type D and shares with that type the relatively large stylar canal pores on the surface of the style apex relatively near its periphery. Style Type B is the most common type in Central America, known in at least 70 species. One species, *P. tripartitum,* though usually having Type D styles, also has Type B and E styles in some populations of the species (see that species for a discussion of its style types).

Style Type C (Fig. 469B) is characterized by being decidedly concave or funnel-shaped at the apex with no lobes on the margins of the rim and with the stylar canals arising in a narrow cluster at the base of the compitum (funnel). Since the stylar canals are closely clustered there is no central dome (defined as any stylar tissue that lies above the level at which the stylar canals emerge onto the style surface). In contrast to style Types B and D, both of which have rather prominent stylar pores, the stylar pores of Type C are small, sometimes barely visible, and in a generally smaller circle nearer the middle of the style apex. This style type is rare in Central American *P.* subg. *Philodendron,* and is known primarily in *P.* subg. *Pteromischum.* Only five taxa of *P.* subg. *Philodendron,* (*P. correae, P. cotonense, P. ligulatum* var. *heraclioanum, P. straminicaule,* and *P. warszewiczii*) have exclusively Type C styles. Though their pistils are funnel-shaped at the apex, these species have funnels generally not as deep as those of *P.* subg. *Pteromischum* as illustrated by Mayo (1989). One other species, *P. radiatum,* has at least one collection (*Croat & Hannon 63414*) with the

style type that also has a funnelform apex and looks like a Type C style. While the dried style of this collection is distinct and button-like, the pores are central in a shallow concavity.

Style Type D (Fig. 469C) is similar to Type B in that it lacks a compitum and has thick stylar canals emerging in a circle on a flat stylar apex relatively close to the margin of the stigma apex. It differs from Type B in that the style is constricted around the circumference to form a protruded flat "style boss" (defined as a ± domed, circular, stigma-bearing projection that extends beyond the main part of the style and is separated from it by a short neck) that rises above the general level of the style apex. Thus the style appears to have a short flat neck at the apex. It is from the "style boss" that the stylar canals emerge. The stylar pores are relatively large and borne relatively near the margin of the style apex. At least 23 species of *P.* subg. *Philodendron* in Central America have Style Type D, the second most common style type.

It is easy to confuse or misinterpret Style Types B and D if the specimens are not well preserved, especially if the material studied is not fresh but rather rehydrated. Species with Type B styles sometimes have styles that dry with a button-like apex resembling that of Type D. At least one collection of *P. advena* has both Type D and Type B styles. Some populations of *P. tripartitum* have not only Type D styles but Type B and Type E as well (see the discussion of that species for details).

Style Type E (Fig. 469D) has a slender funnel-shaped to cylindrical compitum with a distinct raised annulus around the upper rim. The stylar canals arise in a small cluster at the base of the compitum just as in Type C styles. The latter differ, however, in lacking the rim on the style apex. Type E styles are rare in Central American *P.* subg. *Philodendron*, found in only *P. granulare* and perhaps *P. smithii*. *Philodendron granulare* has such an unusual form of the Type E style that it should perhaps warrant its own status. In *P. granulare* the annulus of the stylar funnel actually protrudes well above the surface of the style (at least in its dried state). *Philodendron smithii* was reported by Mayo (1989) as having a Type E style, but no rim is obvious in fresh material of the species. It is more appropriately a Type C style. *Philodendron tripartitum*, though usually with Type D styles, has Type E styles in some parts of its range (see the discussion following that species for details).

Style Type F is narrowly funnel-shaped with a small dome at the base of the compitum around which the stylar canals arise. This type is not known among the Central American *Philodendron*. It is known only from *P. burle-marxii* G. M. Barroso, a member of *P.* sect. *Baursia* (Mayo, 1989) from Amazonian Brazil.

Mayo (1989) has shown that the course of individual stylar canals is correlated with the type of placentation. Those species with basal or sub-basal ovules, such as *P. tripartitum* and *P. smithii*, have stylar canals that course down the center of the axis of the pistil and enter the locule near its base. Those species with axile placentation have stylar canals that also course down the pistil axis and enter the locule somewhere above the base of the locule, but only rarely at the very apex. The stylar canals are lined with papillose epithelial cells, which are contiguous with the stigmatic epidermis (Mayo, 1989). These secrete the gelatinous mucous that keeps the stigmatic surface moist.

FRUITS AND SEEDS

In *Philodendron* the developing pistils remain within the reclosed spathe after anthesis and pollination until they are fully ripe [except in the rare case of *P. surinamense* (Miq.) Engl., a South American member of *P.* subg. *Pteromischum* that promptly loses its spathe after anthesis]. The spathe enlarges somewhat to accommodate the enlarging berries. When the berries are mature the spathe once more begins the process of reopening, but it breaks completely free at the base where it is obliquely attached to the peduncle. Sometimes the spathe falls completely free after loosening even before it opens, but in general it breaks up beginning at the base and falls off (Fig. 33) eventually falling completely free and leaving a scar just above the peduncle (Fig. 34). Generally the old, withered staminate portion of the spadix falls free at this time as well and the berries are exposed on the remaining pistillate portion of the spadix (Fig. 33, *Philodendron hebetatum*). In the process of unfolding, the spathe often develops deep longitudinal fissures, which apparently enable it to unfold. Sometimes the old persistent spathe persists on the peduncle with fragments of the inner surface exposed (Figs. 35, 36).

The berries of *Philodendron* are cylindrical to obovoid, generally with a thickened cap-like apex and not markedly colored, though berry colors from pale yellow to bright orange or even red to purple

do exist (see section on berry color). Berries in *P.* subg. *Philodendron* are universally soft and fleshy except for the frequently thickened apex. The seeds can be seen easily through the sides of the berries. When fully mature the apical portion of the berry is easily torn free, and the thin, fragile sides of the berries are easily ruptured (see section on seeds).

Though little is known about fruit dispersal, the mesocarp surrounding the seeds contained within each locule is juicy or gelatinous and is usually sweet and sticky, making it logically animal dispersed. Infructescences that appear to have been pecked apart by birds (Fig. 36) are frequently seen. Certainly the sticky seeds, often many per berry, would logically be easily dispersed on birds' beaks. Alternatively, the infructescence is large, and even faintly scented when fully mature, making it an appealing meal even for mammals such as monkeys. Grayum (1996) theorized that those species of *P.* subg. *Pteromischum* with whitish fruits, which may produce a garlic-like or pepper-like odor at night, are dispersed by bats. Those with orange fruits may be dispersed by diurnal animals. Certainly the manner in which many species of *P.* subg. *Pteromischum* flower, e.g., on the ends of short, spreading branches some meters above the ground, would make them superbly positioned as bat fruits. There are also species of *P.* subg. *Philodendron*, such as *P. lentii*, which have their branches held in a similar manner.

Ants are also probable dispersers of *Philodendron* seeds. I have seen two different species of ants carrying away individual seeds of *Philodendron*. Ant dispersal is certainly important for those species, such as *P. megalophyllum* in South America, that live almost exclusively on ant nests. One cultivated individual of that species even set fruit repeatedly without being pollinated. Doing so in nature would provide a steady, abundant supply of berries for its ant dispersers and assure the species widespread dispersal. Indeed, the species is particularly successful even in areas of white sand soil where soil nutrients are very low.

Although berry color is known for only a relatively small number of *Philodendron* species (53 out of 96), some general comments can be made. Berry color in *Philodendron* is not so important taxonomically as it appears to be in *Anthurium* (Croat, 1983a, 1986a, 1991). Grayum (1996) reported that for *P.* subg. *Pteromischum* the fruits sometimes provided taxonomically significant characters, with species related to *P. inequilaterum* having orange fruits while other species have whitish fruits.

Mature berries of most *Philodendron* species are generally described as "white," but are usually more nearly ochraceous or somewhat greenish white. A total of 33 species have either white, creamy white, or greenish white fruits at least some of the time. In some species, such as *P. advena* and *P. smithii*, the whitish berries turn somewhat yellowish when fully mature, and the mature fruits of *P. brevispathum* are pale yellow. The berries of *P. sagittifolium* are usually pale yellowish but rarely have been reported as orange. While the majority of *Philodendron* berries are whitish, 17 species of Central American *P.* subg. *Philodendron* are known to have berries at least sometimes pale orange to orange. An additional three species have yellow or yellowish berries. *Philodendron fragrantissimum* has bright red to purple-red berries.

Known species with orange fruits are members of *P.* subsect. *Glossophyllum*. These are: *P. auriculatum*, *P. bakeri*, *P. cotonense*, *P. pseudauriculatum*, *P. wendlandii*, and *P. wilburii*. Other species with orange fruits are *P. anisotomum*, *P. brenesii*, *P. crassispathum*, *P. ferrugineum*, *P. lentii*, as well as, at least sometimes, *P. jacquinii* and *P. sagittifolium*. Three of the above, *P. brenesii*, *P. crassispathum*, and *P. lentii*, are members of *P.* ser. *Ecordata*. Thus, it may be significant that most species with decidedly orange fruits are members of *P.* sect. *Calostigma*. Even *P. ferrugineum*, with orange berries, and *P. sagittifolium*, sometimes with orange berries, are members of *P.* sect. *Calostigma*. Only *P. anisotomum* (*P.* sect. *Tritomophyllum*) and *P. jacquinii* (*P.* sect. *Macrogynium*) are not members of *P.* sect. *Calostigma*.

The seeds of *P.* subg. *Philodendron* are few to many per berry and are mostly oblong to oblong-ellipsoid, ellipsoid, ovoid-oblong, or less frequently ovoid. Typically they are minute (see below). The seeds are typically more or less terete, though they may be somewhat flattened, e.g., in *P. findens*. They have a rather thick, smooth (e.g., *P. granulare*) or striate-costate testa, as well as copious endosperm. The longitudinally oriented striations may be weak (*P. advena*, *P. findens*, *P. cotonense*, *P. purpureoviride*, and *P. sagittifolium*) to strong (*P. ferrugineum* and *P. grandipes*). Seeds of *Philodendron microstictum* have both longitudinal striations and much finer cross-etching. A number of species are reported to have seeds with pale raphide cells on the surface. These include *P. hederaceum* and *P. warszewiczii*. Seeds of some species, e.g., *P. anisotomum* and *P. hederaceum*, sometimes have a constriction on the end opposite the funicule.

Philodendron seeds are usually dramatically smaller than those of *Anthurium*, which typically have only two seeds per berry. Seeds of species of *P.* subg. *Philodendron* studied (a total of 48 species)

ranged from 0.5 mm to 5 mm and averaged 1.67 mm long; seed diameter ranged from 0.1 to 3 mm, averaging 0.7 mm. The longest seeds were those of *P. jacquinii* and *P. hederaceum*, at 5 mm. Relatively few species have seeds longer than 2 mm: *P. advena*, *P. anisotomum*, *P. findens*, *P. dolichophyllum*, *P. grayumii*, *P. purulhense*, *P. rothschuhianum*, *P. sagittifolium*, and *P. warszewiczii*.

The number of seeds in each locule is often many fewer than the average number of ovules per locule, presumably owing to the fact that not all are properly pollinated. A careful examination sometimes shows the aborted undeveloped ovules that were present at the time of flowering. The percentage of ovules in each locule that develops into seeds varies from species to species. Species of *P.* sect. *Calostigma* that have only one or a few ovules per locule are more likely to have an equal number of seeds. On the other hand, species in *P.* sect. *Philodendron*, especially those with large numbers of ovules per locule, rarely develop all their ovules.

Because species of *P.* sect. *Calostigma* have fewer ovules per locule and thus fewer seeds, one might expect them to have larger seeds. Though admittedly the sample size was small (only 21 species studied for *P.* sect. *Calostigma* and 17 for *P.* sect. *Philodendron*), the unexpected results were that the seeds of species of *P.* sect. *Philodendron* in Central America averaged slightly larger than those of *P.* sect. *Calostigma* (to 1.69 mm long for *P.* sect. *Philodendron* and to 1.66 for *P.* sect. *Calostigma*).

Philodendron seeds are largely pale in color, mostly shades of brown, tan, or white, though for most species mature seeds have not been observed. Seeds vary in color from medium green (*P. rothschuhianum*) to whitish (*P. roseospathum*), tan (*P. alticola*, *P. annulatum*, *P. granulare*, *P. morii*, *P. smithii*), yellowish or pale yellow (*P. brenesii*, *P. llanense*, and *P. strictum*), yellow-orange (*P. crassispathum*, *P. purpureoviride*, *P. wilburii*, and *P. mexicanum*), brown (*P. ferrugineum*), or reddish brown (*P. heleniae*). The dried seeds of two species, *P. findens* and *P. jefense*, are described as translucent.

Pollination Biology

Although there are frequent insect visitors to *Philodendron*, especially small Hemiptera in the genus *Neelia*, which appear not to feed or mate on the inflorescences (H. Young, pers. comm.), only the larger beetles are known to be pollinators. The system of pollination is nearly identical to that of *Dieffenbachia* (Croat, 1983b; Young, 1986, 1990). Pollinators are members of subfamily Dynastinae in the family Scarabaeidae (Fig. 32). All determined beetles collected from either Central American or South American *Philodendron* are members of the genera *Cyclocephala* and *Erioscelis*. Some species of beetles are not particularly host-specific, visiting members of both *P.* subg. *Philodendron* and *P.* subg. *Pteromischum*; other genera such as *Dieffenbachia*, *Homalomena*, *Syngonium*, and *Xanthosoma*; and sometimes even other families including some palms (Arecaceae), *Cyclanthus bipartitus* Poit. ex A. Rich (Cyclanthaceae), as well as *Annona* and *Cymbopetalum* in the Annonaceae (M. Grayum, pers. comm.; Schatz, 1990). *Cyclocephala negerrima* Bates, for example, has been found visiting *P. brenesii* and *P. tysonii*, but also *P. standleyi* Grayum, a member of *P.* subg. *Pteromischum* (see Table 3). Though beetles are not very species-specific pollinators, individual beetles of some species tend to be somewhat stratum-specific, visiting only those species growing at particular height ranges above the ground (Schatz, 1990; Helen Young, pers. comm.). These beetles are attracted to the *Philodendron* inflorescence, usually late in the day or at dusk. Attractants and/or rewards are apparently a combination of scent (at least in many cases), a source of food (oil-bearing sterile staminate flowers), warmth (thermogenesis), and shelter.

Scents produced by *Philodendron* species are not always obvious, at least in *P.* subg. *Philodendron*. George Schatz and Helen Young (pers. comm.) have documented floral odors for species of *Philodendron* and have identified the principal constituents of these aromas. Some species have noticeably sweet aromas in the early evening hours, while other species have no noticeable scent, at least during the early evening hours on the first day of anthesis. *Philodendron megalophyllum* (in cultivation at the Missouri Botanical Garden), a South American species, had a faint spicy aroma detectable directly at the spathe during the evening, but even this faint aroma was absent the following morning on day two of the flowering event. At the same time the stigmas were soft, juicy, and sticky but without an obvious flavor or taste both in the evening and the following morning. Schatz (1990) believed that the pattern of visitation to *Philodendron* exhibited by beetles at La Selva in Costa Rica was to a great degree explained by odor. He pointed, for example, to the high degree of specificity exhibited by *Philodendron radiatum* and an undescribed species of *Cyclocephala*. The aroma given off by *P. radiatum* was made up of compounds unique to that species.

At anthesis the open spathe of *Philodendron* provides ample space at the base in the area surrounding the pistillate portion of the spadix. The spathe

blade may provide a certain amount of protection against rain, as mentioned previously. Beetles typically spend the first night and most of the following day inside the spathe where they remove the sticky exudate from the pistils, eat pollen (Gottsberger & Silberbauer-Gottsberger, 1991), feed on the sterile staminate flowers, and mate. Studying *P. bipinnatifidum*, Gottsberger and Silberbauer-Gottsberger (1991) found that the beetles were active mostly during the first 10 to 20 minutes after arrival and during the strongest production of scent. Copulation was most active immediately after arrival, when the spadix was warmest; grazing on the sterile male flowers also subsided by the time the spadix had cooled off. Old inflorescences that have been pollinated often have the sterile staminate portion of the spadix entirely eaten away.

Typically the number of beetles found in a single inflorescence is modest, frequently no more than five and sometimes up to a dozen beetles. However, sometimes the numbers are simply astounding, with Gottsberger and Amaral (1984) reporting as many as 200 beetles in a single inflorescence of *P. bipinnatifidum*. While visiting beetles are often of the same species, sometimes more than one species of beetle may be found in the inflorescence. Though beetles typically do not leave the spathe until about dusk, they will leave if the inflorescence is sufficiently disturbed. When beetles are disturbed, they may crawl slowly up the spathe or spadix and appear at the rim of the open spathe, at which point they generally fall promptly to the ground where they disappear in the leaf litter or soil with remarkable speed.

Thermogenesis, the production of heat in the spadix by the rapid oxidation of stored starch or lipids (Walker et al., 1983; Gottsberger, 1990), plays an important role in the pollination of *Philodendron* (van Herk, 1937a–c; Van der Pijl, 1937; Knutsen, 1974; Seymour et al., 1984). Gottsberger (1984, 1986), studying *P. bipinnatifidum*, has shown that, although oxidation of carbohydrates takes place during preheating of the spadix, lipids are oxidized thereafter during maximum heating and are consumed directly, not after conversion to carbohydrates. This makes the biochemistry of this species similar to that accompanying heat production in some animals. The thermogenic reaction occurs principally in the staminodial region of the staminate portion of the spadix (James & Beevers, 1950; Henry & Nyns, 1975) involving the inner surface of mitochondrial membranes (Urdentlich et al., 1991) and is triggered by an accumulation of salicylic acid (Meeuse & Buggeln, 1969; Raskin et al., 1987, 1989; Meeuse, 1975, 1978; Raskin, 1992). The end result of this high rate of respiration in these plants is the production of heat rather than ATP as in animals (Meeuse, 1966). To accomplish this high increase in metabolism the plant's mitochondria in the inflorescence switch to an electron transport pathway commonly referred to as the "cyanide-resistant pathway."

The thermogenetic heat rise in *Philodendron* is sometimes dramatic, with temperatures rising well above ambient temperature (Nagy et. al., 1972; Knutsen, 1974). Gottsberger and Silberbauer-Gottsberger (1991), working with *P. bipinnatifidum*, reported temperatures of spadices occasionally to 46°C with the highest and most efficient temperatures for the emission of scents being maintained for 20–40 minutes. Thermogenesis does not create even or constant temperatures, but rather produces fluctuations depending on the time of day with definite peaks (Leick, 1910, 1916; Engler, 1920a, 1920b; Foster, 1949; Nagy et al., 1972; Sheridan, 1960; Gottsberger & Amaral, 1984), the greatest occurring when beetle visitation and odor is most intense (Gottsberger & Amaral, 1984). Temperature peaks may occur on two or more successive days. While the increased temperature is presumably responsible for the production of scent compounds (Nagy et al., 1972), and whereas the production of heat and scent appears closely correlated with peaks in temperature, there is still controversy over the exact function of the heat production at least as it pertains to genera that produce foul odors. Moodie (1976) suggested that heat production and the higher levels of carbon dioxide production are components of a carrion, dung, and mammal mimicry syndrome and that heat production aids in providing sufficient warmth in colder climates for the activity of pollinating organisms. The subject of thermogenesis and its role in pollination has been reviewed in great detail by Mayo (1986), Grayum (1990), and Bay (1995[1996]).

The exact role that thermogenesis plays in the pollination of *Philodendron* is still poorly known, and rather few plants have been studied on an experimental basis. Despite its probable occurrence in all *Philodendron* species, thermogenesis has thus been documented only for *P. selloum* K. Koch and *P. bipinnatifidum*, now considered by Mayo (1991) to be synonymous. My own measurements with a recording thermometer on *P. glanduliferum* and *P. advena* in the field in Chiapas, Mexico, indicated a definite heating during the early evening hours, usually peaking between 18:00 and 19:00 hours.

The site of the heat production on the spadix is another possible difference between *P.* subg. *Meconostigma* and *P.* subg. *Philodendron*. Mayo's

(1986) investigations on *P.* subg. *Meconostigma* indicated that heat production was centered in the sterile staminate section of the spadix. In *P.* subg. *Meconostigma*, that section is as large as or larger than the fertile staminate part of the spadix, a situation unknown in *P.* subg. *Philodendron* where the staminodial segment is always a small percentage of the total spadix.

Contrary to Mayo, Leick (1916) reported that heating took place in the "middle and upper part" of the spadix in *P. selloum*, presumably implying at least a part of the fertile staminate portion. Concurring with this view, Ron Weeks (pers. comm.) reported that a perceived temperature rise occurred in both the sterile and fertile staminate spadix portions of those species of *P.* subg. *Meconostigma* that he studied. Mayo (1986) theorized that, because of the major morphological differences in the relative lengths of the sterile and fertile staminate portions of the spadices, the two subgenera would likely have different thermogenetic patterns.

In the Central American *Philodendron* species observed by the author, the spathe opens broadly late in the afternoon of the first day of flowering; it closes slightly the morning after the first night of anthesis. The evolutionary significance of this slight closure is uncertain but, even in the most extreme cases, it occludes only the pistillate portion. The spathe continues to close on the evening of the second day after having been open for about 24 hours (see discussion below). The beetles, which generally enter the spathe on the first night of opening, spend about 24 hours in the spathe tube. This second partial closing process usually corresponds with staminal dehiscence. The now crowded condition of the spathe tube, and the probable desire on the part of the beetles to seek a new food source with the onset of dusk, encourages the beetles to leave the inflorescence. The beetles emerge from the spathe tube by either climbing up the side of the spadix or up the inside wall of the spathe. By the time they emerge from the spathe, it is quite constricted and they must squeeze through the constriction which fits rather tightly around the spadix just above the sterile staminate portion. In order to depart the beetles must literally crawl through the copious strands of pollen that emerge from the apical pores of the stamens. The constriction of the spathe and its corresponding constricted area on the spadix help to insure that most of the pollen that falls into the spathe tube accumulates and is carried forward and out of the spathe by the departing beetles. Araceae pollen is not very tacky and probably does not adhere well to the smooth, hard surfaces of the beetles. However, the beetles themselves are usually quite sticky from the sugary secretions of the styles and especially from the resin, which arises usually from the inner surface of the spathe or sometimes from the spadix itself (Fig. 128). Once the beetles have emerged they fly off in search of another place to spend the night, usually another open inflorescence. The beetles apparently have a keen perception of infra-red radiation or of scent because they are often seen in a "homing-in" pattern, which is quite direct to the next available inflorescence (John Rawlins, pers. comm.). Gottsberger and Silberbauer-Gottsberger (1991) reported that beetles flew in a zig-zag pattern toward the center of fragrance concentration, indicating that they were very sensitive to the aroma being produced. They also reported that once the beetles were within sight of the inflorescence they shifted to a straight line of flight until they hit the inner surface of the spathe blade, whence they moved into the lower portion of the spathe. Gottsberger and Silberbauer-Gottsberger (1991) have proven experimentally in the case of *P. bipinnatifidum* (a member of *P.* subg. *Meconostigma*) that the beetles use only visual references for location as they near the inflorescence. Shelter, warmth, food, and copulation are the driving forces behind this pollination strategy, and although selectivity is not perfect in such beetle-pollinated systems (Young, 1986, 1988a) fruit-set in undisturbed populations is high. The precision and high degree of synchrony of thermogenesis gives evidence of a highly evolved system of pollination.

Even though all detailed observations thus far have been made with *P. bipinnatifidum*, there is considerable confusion regarding the results. Horticulturist Ron Weeks (Homestead, Florida) reported (pers. comm.) that three members of *P.* subg. *Philodendron*, *P. bipinnatifidum*, *P. speciosum* Schott, and *P. williamsii* Hook. f., showed no variation in the schedule of spathe opening, the capability of the plants being hand-pollinated on the first evening of opening, or in the shedding of pollen on the evening of the second day. On the other hand, he reported that *P. eichleri* Engl. showed great variation in opening periods, temperature changes, fragrance, and pollen shed, perhaps owing to weather conditions. Scientific studies carried out on other plants in *P.* subg. *Meconostigma* showed considerable variability. Four separate and conflicting reports were made on material determined as belonging to *P. bipinnatifidum* in Brazil. Warming (1867, 1883) reported a two-day pollination event with two heat peaks (early evening and late morning, respectively) with the spathe closing then reopening during the first night. Gottsberger and

Amaral (1984) reported on two plants, one as *P. selloum* (now considered to be a synonym of *P. bipinnatifidum*) with a three-day pollination event with two unequal early evening heat peaks, and one as *P. bipinnatifidum* with a four-day pollination event with three unequal early-evening heat peaks. The spathe was not reported to close during the event. Confirming the complexity of the thermogenesis riddle is the fact that Seymour et al. (1983), studying a cultivated but similar plant believed to be the same species (Mayo, 1986), found both types of pollination events that had previously been described by Gottsberger and Amaral but this time in a single plant. Clearly more investigation must take place, at least in *P.* subg. *Meconostigma*, to determine the pollination behavior.

Leick (1916), reviewing work done by Kraus (1894, 1896) with *P. bipinnatifidum*, a member of *P.* subg. *Philodendron* from Venezuela, reported a two-day pollination event with temperature peaks in the evening of two consecutive days. While it is not certain that most Central American *Philodendron* have an elevated temperature on two consecutive days, the general pattern of opening and closing of the spathe and the beetle visitation in *P. bipinnatifidum* would appear to match the events of Central American species observed in the field and under greenhouse conditions at the Missouri Botanical Garden. Further detailed studies of this phenomenon, including a much broader survey of Central American species, will be carried out by my student, Jane Whitehill, during graduate studies at the Missouri Botanical Garden.

Grayum's (1996) observations with *Philodendron* subg. *Pteromischum* showed a similar pattern, with most species having the spathe beginning to loosen by early afternoon and being fully open by mid-afternoon. He reported that for the species of *P.* subg. *Pteromischum* he observed, the pollinators appeared at the opened inflorescence during a relatively brief time, usually between 19:00 and 19:15 hours. An important feature in the pollination story reported by Grayum (1996) for the first time is that resin secretion from the inner spathe surface does not begin until 21:00 to 22:00 hours on the first day of anthesis, and that it then continues until the end of anthesis.

Once opened, the spathes of *P.* subg. *Philodendron* apparently remained open during the night and were always open the next morning at the beginning of day two, remaining open during the course of most of the day. During the latter part of the same day, usually in late afternoon of day two, the spathe began to close and pollen began to shed in long filaments. The spathe did not fully close at this time but remained open near the apex. It remained in this condition into the beginning of the evening of day two. By the beginning of day three the spathe was generally fully closed, and the only evidence that it had ever opened was often some loose pollen remaining on the closed edges of the spathe. In addition, the closed spathe is somewhat less turgid than before anthesis, sometimes allowing it to be forced open without breaking the margins of the spathe. Doing the same with an unopened spathe is impossible without breaking the stiff and brittle spathe margins.

The entire pollination episode usually requires little more than 24 hours, counting just the time that the beetles are present. The time that the spathe is to any extent open could be as much as 8 hours longer, since it may open late in the afternoon and remain open for some hours after the pollen has been shed. Grayum (1996) reported that for the species of *P.* subg. *Pteromischum* studied in Costa Rica the average pollination event required about 30 hours (i.e., from spathe opening to closing).

That the intensity of light must play an important role in flowering behavior is indicated by the fact that on cloudy days spathes in cultivated collections open earlier than usual, sometimes as early as noon on day one of the flowering sequence. This may support the argument of Buggeln et al. (1971) that darkness induces opening of the spathe and an elevated respiration rate in *Sauromatum venosum* Kunth.

Armbruster (1984), studying the role of resin in angiosperm pollination, has questioned the efficacy of floral resin in the transport of pollen, citing its possible toxicity and the difficulty of transporting pollen embedded in resin. While he stressed the role of resin for other purposes, mainly in nest-building by bees, it must be pointed out that bees which use resin for nest building play no role whatever in *Philodendron* pollination. In contrast, the general availability of resin, its close association with pollen delivery, the non-tacky nature of *Philodendron* pollen, and the availability of resin only at anthesis all point to a strong role for resin in *Philodendron* pollination. In species with resiniferous spadices (Fig. 128), the pollen is shed with and incorporated in the resin from the moment of theca dehiscence. Alternatively, species that lack staminal resin and instead have resin only on the inner spathe surface have pollen presented as slender filaments.

Breeding studies (see section on Breeding Behavior) have shown that *Philodendron* species have few if any genetic barriers to cross-pollination, ow-

ing perhaps to the fact that there are other physical and temporal barriers to self-pollination. Even when two species of *Philodendron* are in flower simultaneously, there are other parameters that effect separation. Beetles tend to fly at certain elevations above the ground (Schatz, 1990), helping to prevent cross-pollination of species that flower at different strata. In addition, specific attractants, i.e., species-specific pheromones, may exist in some species that attract principally a single beetle species (H. Young, pers. comm.). The sloppiness in the system, when it occurs, is owing to opportunistic beetle visitors (G. Schatz & H. Young, pers. comm.), and this might produce some hybridization.

Perhaps because of the substantial barriers already present, *Philodendron* appears to have developed the ability to cross between sections. In *Anthurium*, relatively little cross-breeding was possible between different sections in the genus (Croat, 1991). In contrast, quite unrelated species of *Philodendron*, even species in different sections, readily cross-pollinate and produce intermediate offspring (Keith Henderson, Cairns, Queensland, Australia, pers. comm.). For this reason pre-zygotic separation may be critical to maintaining distinct species lines. The pollinators of *Philodendron*, dynastine scarab beetles, are for the most part not very species-specific and frequently switch from one species to any other in flower at the same time. Not only will some species of beetles switch from one *Philodendron* species to the next, as is known for certain in *Dieffenbachia* (Young, 1986), but some individuals will also switch to another genus. For example, beetles that regularly visit *D. longispatha* Engl. & K. Krause at La Selva may visit *P. grandipes*, another species that is terrestrial and about the same height above the ground (G. Schatz & H. Young, pers. comm.). Beetles are also reported to move from *Dieffenbachia longispatha* to *Xanthosoma undipes* (K. Koch & Bouché) K. Koch. Some individuals of beetle species that regularly visit *D. longispatha* will even switch to *Cyclanthus bipartitus* Poit. (Cyclanthaceae). Schatz believes that this is owing to the fact a small component of the pheromone emitted by *Cyclanthus* Poit. ex A. Rich is the principal component of the scent given off by *Dieffenbachia longispatha*. He believes that during the end of the flowering season of *Dieffenbachia* and the beginning of the flowering season of *Cyclanthus* some confusion occurs in the pollinators' behavior.

The unpublished observations of G. Schatz and H. Young (pers. comm.), and the published results reported by Helen Young (1986, 1988a, 1988b) principally for *Dieffenbachia*, probably are comparable to what is happening in *Philodendron*. Beetles that visit any particular species of *Dieffenbachia* are often predominantly of one species, but they are often accompanied by other opportunistic beetles. Schatz believes that these opportunistic species are not likely to be effective pollinators, since they are so catholic in their tastes that they are not likely to make their next visit to a receptive *Dieffenbachia*. Likewise, Helen Young (Young, 1988a) indicated that the most common species of beetles are not the most effective pollinators. However, they may be responsible for the occasional hybrids seen in *Dieffenbachia*, at La Selva, where the studies of both Schatz and Young were carried out. The pollination system described for *Dieffenbachia* by Young and Schatz is apparently similar to that of *Philodendron*. Schatz (pers. comm.) reported that while one undescribed beetle species (determined as *Cyclocephala ampliata* by H. Young), was found to visit only *Philodendron radiatum*, it was accompanied occasionally by another more opportunistic species. Despite the presence of opportunistic beetle species, some beetle pollinators of *Philodendron* species are probably much more species-specific. For example, Grayum (1996), citing unpublished data collected by George Schatz, reported that two unrelated species of *Philodendron* subg. *Pteromischum* were pollinated by the same species of beetles, and that both *Philodendron* species have floral odors featuring the same two principal components. This leads to the conclusion that there is a degree of specificity among pollinators for certain species based on their floral odors. In addition, in the list of pollinators known for *P.* subg. *Philodendron* (see Table 3), only three *Philodendron* species were observed to have more than a single species of beetle present at any one time. In each case, two species of beetles were present. As can be seen from *P. grandipes* (Table 3), the beetle species need not always be the same. Though more studies must be made on pollination biology of *Philodendron*, and even though the beetle pollination system is somewhat sloppy and imprecise, a combination of a moderately strong beetle-plant specificity, coupled with severe phenological constraints and narrow windows of pollination opportunities (perhaps as little as a few hours per year), works to reduce interspecific hybridization. Although hybrids can be readily produced under greenhouse conditions, evidence for hybridization is not usually apparent among wild populations.

BREEDING BEHAVIOR

In comparison to *Anthurium*, where breeding studies were easy to conduct (Croat, 1980, 1983a,

1986a, 1991), *Philodendron* pollination was difficult. Cross-pollination attempts were easy in *Anthurium* owing to their hermaphroditic flowers and because plants often had several inflorescences per plant in different stages of development. In addition, the plants reached anthesis during the day when greenhouse personnel and volunteers were available to make cross-pollinations. In *Philodendron,* the number of inflorescences available was always fewer than in *Anthurium*; *Philodendron* sometimes produced only a single inflorescence per season. In addition, *Philodendron* was very seasonal in its flowering behavior (unlike *Anthurium,* which sometimes flowered all year), making pollination all the more difficult. When flowering did occur it was often unexpected since it is difficult to tell when the spathe is ready to open. Moreover, the spathe generally opens for one day only. Opening usually took place late in the afternoon after greenhouse personnel left. Even if the opening inflorescence was found in time, it was generally impossible to find another plant with fresh pollen to use for purposes of experimental crosses. *Philodendron* pollen does not remain viable very long, though it can be kept viable for a time in glassine envelopes. Ron Weeks, a grower from Homestead, Florida, reports (pers. comm.), that he stores pollen in film canisters at refrigerator temperatures and that it remains viable for several weeks. He also reports that inflorescences cannot be pollinated after the first evening they open. After the spathe opens (generally late in the day) it is only during the evening and night of the first night that the pistillate flowers are believed to be receptive. Attempts to pollinate plants with their own pollen have always failed if one waits until the pollen emerges. It should be noted, however, that Grayum (1996) reported that, based on the use of peridoxase paper, which purportedly indicates the receptivity of stigmas (Young, 1986), the stigmas were receptive for up to 24 hours after anthesis. Though it seems unlikely that pistillate flowers are receptive after the first evening of anthesis, the pistillate flowers are receptive for an unknown period of time before the spathe opens, so that most successful pollinations usually involved cutting a hole in the spathe after obtaining very fresh pollen from a plant in the staminate phase of flowering. Though one can completely remove the spathe then protect the developing pistils with a plastic bag, it is better to simply cut a window in the spathe large enough to see most of the spathe. Then with a small brush one can spread pollen over as many of the pistils as possible, again covering the spathe for a time with a plastic bag to insure that the pollen does not dry out and fail to germinate. An effective means of spreading the pollen to insure adequate and uniform coverage is to mix the pollen with water.

Failure to remove or at least loosen the bag used to cover the pollinated spadix later may result in mold developing in the spathe. Unpollinated inflorescences usually fall off within a week or two. Ron Weeks (pers. comm.) reported that for *P.* subg. *Meconostigma* in Florida the unpollinated inflorescences may persist for up to a month. Development time for fruits ranges from only a few weeks or more generally a few months and sometimes nearly a whole year. Ron Weeks (pers. comm.) reports that in *P.* subg. *Meconostigma* fruits ripen in South Florida in 2.5 to 3 months.

Phenology

Based on a field-oriented study of phenology and pollination behavior carried out at La Selva in Heredia Province, Costa Rica, Grayum (1996) reported species of *P.* subg. *Pteromischum* flowered for periods of 4–8 weeks. Obviously, since most members of *P.* subg. *Pteromischum* have only one or two inflorescences per axil, vs. sometimes 4 or more for *P.* subg. *Philodendron,* the flowering episodes of the latter might be longer than two months. The flowering events, however short or long, are not necessarily the same year after year. I suspect that, like understory vegetation (Croat, 1975), their flowering phenology may be affected by the onset of the rainy season.

Based primarily on a phenological survey of herbarium collections, flowering (and to a lesser extent fruiting) behavior has been studied here for Central American species of *P.* subg. *Philodendron.* These studies resulted in a phenological statement for each species. This statement follows the description of each species as a part of the discussion. Some general comments regarding phenology are important.

In studying herbarium material for phenological variation it is often difficult to determine the exact state of the inflorescence. However, with experience it is relatively easy to distinguish inflorescences that have never opened, i.e., pre-anthesis, from those which have already opened. Spathes that have never opened are very tightly closed, whereas those that have already undergone anthesis are not so tightly closed. By dissecting the spathe one can quickly determine if the pollen has emerged. If so, the spathe has already opened and reclosed over the spadix.

Spadices at anthesis when they are collected are usually easy to discern as well because they are

typically opened when pressed. It is difficult, however, to easily predict the age of an inflorescence beyond anthesis and before swelling due to the enlargement of the pistils. Since an inflorescence at anthesis is rare (open less than 24 hours), while every successfully pollinated inflorescence persists for one to many months, there will always be many more collections with "post-anthesis" inflorecences than those described as "in flower."

Central American members of *P.* subg. *Philodendron* fall into several phenological groups. All of these categories can have variations, and flowering is rarely consistent throughout any period. Some categorizations are tentative, as listed in Appendix 4, "Phenological Patterns of Central American *Philodendron* subg. *Philodendron*."

The flowering patterns of Central American members of *P.* subg. *Philodendron* are as follows:

A. FLOWERING IN DRY SEASON AND WET SEASON

This is the largest flowering category among Central American *P.* subg. *Philodendron*. A total of 47 species fall into this category, including *P. fragrantissimum, P. panamense, P. sagittifolium, P. grandipes, P. pterotum,* and *P. radiatum*. Although these species begin flowering during the dry season, the dry season rarely constitutes the period of greatest flowering activity (except perhaps in the case of *P. hederaceum*, a species which though apparently flowering all year and thus aseasonal appears to have more flowering collections made during the dry season than at any other time of the year). Low flowering activity is particularly characteristic of species inhabiting regions of *Tropical moist forest* or other areas where marked seasonal changes are apparent and affect the availability of beetle pollinators.

Those species occurring in cloud forest habitats (usually *Premontane rain forest* or *Lower montane wet forest*) also seem to have more flowering in the rainy season even though they are more apt to be in flower in the dry season than their *Tropical moist forest* counterparts.

Though perhaps it is merely a matter of poor sampling, species more common, widespread, or locally abundant tend to have flowering seasons that extend from the dry season to the wet season, whereas rare species seem much more likely to have flowering restricted to either the dry or the wet season.

B. FLOWERING ONLY IN WET SEASON

This is the second largest flowering category, comprising 30 species (32 taxa) believed to flower exclusively in the wet season (roughly between May and December in Central America). They represent largely rare or narrowly distributed species for the most part and are often species that inhabit the wettest and frequently the coolest forest types such as *Tropical wet forest, Premontane wet forest, Premontane rain forest,* and *Lower montane wet forest.* Examples of species in this flowering type are: *P. albisuccus, P. antonioanum, P. chiriquense, P. coloradense, P. correae, P. cotobrusense, P. dominicalense, P. dodsonii, P. ferrugineum, P. gigas, P. hammelii, P. jefense, P. madronense, P. niqueanum, P. pirrense, P. purulhense, P. squamicaule,* and *P. ubigantupense.*

Not all species that flower exclusively in the wet season occur in very wet or cool forest. A few species flower only in the wet season because the dry season in the region where they occur is often too severe, perhaps so severe as to limit the beetle pollinators. These include several Mexican species, e.g., *P. basii, P. breedlovei, P. dressleri,* and *P. sousae.*

C. FLOWERING ONLY IN DRY SEASON

One of the most unusual flowering categories, and a relatively small one with only 7 species, is a group believed to flower only during the dry season (January to April in Central America). This group is diverse and difficult to characterize. Some of the species, such as *P. bakeri, P. brewsterense, P. chiripoense, P. edenudatum, P. folsomii,* and *P. knappiae,* occur in wet to very wet areas, some in areas where weather conditions are so bad in general during the rainy season that it may be more efficient to compete for pollinators during the dry season (which would not be very dry in any event). *Philodendron dwyeri* is unusual in that it flowered at the beginning of the dry season in an area that in general is quite arid in this season. It is known from only a single individual and may have represented an unusual, out-of-phase flowering.

D. FLOWERING ALL YEAR

Species that flower aseasonally are usually common species such as *P. hederaceum* (though it apparently flowers more frequently in the dry season) and *P. jacquinii* (which is also often edaphically versatile or less subject to the pressures of the environment). Though not as widespread as the two aformentioned species, *P. advena,* another member of this group, is a tough, highly variable and ecologically adaptive species. *Philodendron purpureoviride* has much the same edaphic preferences as *P. hederaceum,* although it is much less widespread.

Both are highly adaptable, scandent species. *Philodendron hederaceum*, though flowering all year, is even more commonly in flower in the dry season than in the wet season. *Philodendron radiatum*, also a member of this group, is as widespread and even more common than *P. hederaceum*.

E. FLOWERING BIMODALLY

Based on the historical record of herbarium collections, only a few species are expected to flower twice per year. This pattern may be much more common and simply masked by the year-to-year variation in flowering behavior. Grayum (1996) reported bimodal flowering to be common with *P.* subg. *Pteromischum*. He indicated that the two modes were quite unequal, that one of them involved far fewer individuals and lasted for a shorter period of time. Among species of *P.* subg. *Philodendron*, *P. aromaticum* appears to flower in the mid-dry season and mid-wet season. It is possible this species is just too poorly known to determine its phenology. *Philodendron morii* may also flower bimodally, with flowering collections seen in March and November, and with immature fruiting collections in December, February, and June. *Philodendron wilburii* appears to flower at the beginning of the dry season and primarily later at the beginning of the rainy season.

Several species are poorly known phenologically because of sparsity of flowering collections: e.g., *P. dominicalense*, *P. niqueanum*, and *P. ubigantupense* (all seen in flower only once during the early rainy season). All of these are assumed to be species that flower entirely during the rainy season.

Fruiting phenology in *Philodendron* subg. *Philodendron* is too poorly known to report on here. Most species appear to develop fruits from between one and four months after the time of pollination, depending on the size of the infructescence, but too few mature fruting collections were observed to determine the phenological period. Fruit development time is affected by the size of the infructescence. Species with small spadices, such as *P. heleniae*, produce mature berries faster than species with larger spadices.

CYTOLOGY

No karyological studies were made for this revision, but Petersen (1989) reviewed all chromosomal literature and made new studies. The chromosomes of *P.* subg. *Philodendron* are small, with counts of $2n = 30, 32, 34$, and 36 (rarely 26 and 48). Petersen (1989) speculated that the base number for the genus is 18. Very few of the 29 species (other names were synonyms or hybrids) for which chromosome counts have been reported are members of the genus from Central America. Those Central American species for which chromosome counts have been reported are: *P. radiatum* $2n = 32$, *P. microstictum* (as *P. pittieri*) $2n = 34$, *P. verrucosum* $2n = 34$, and *P. hederaceum* (as *P. scandens*) $2n = 36$. *Philodendron wendlandii* was counted at $2n = 54$, but Petersen believed this to be either an error in counting or not a *Philodendron*.

GEOGRAPHICAL DISTRIBUTION AND ENDEMISM

The *Philodendron* subg. *Philodendron* flora in Central America is diverse but heavily concentrated in the southeastern part near South America. Despite this, relatively few Central American species actually enter South America. Most species that do enter the South American continent range along the Pacific slope into northwestern Colombia and Ecuador, with relatively few occurring east of the Andes and even fewer entering the Amazon basin.

As was shown for *Anthurium* (Croat, 1983a, 1986a, 1986b), species diversity of *P.* subg. *Philodendron* shows a general diminution from Mexico to Middle America, followed by a marked increase approaching South America (Appendix 3, "Sectional Classification of *Philodendron*"). Distribution of *Philodendron* in Central America is as follows: Mexico has 21 taxa, Guatemala 15, Belize 9, El Salvador 5, Honduras 13, Nicaragua 18, Costa Rica 48, and Panama 82. Thus species diversity is greatest in Costa Rica and Panama, with 46% and 79% of the total Central American species, respectively. Collectively the number of species in these two countries comprises 90% of the species total.

Fifty-three species (58 taxa) of *P.* subg. *Philodendron* (nearly 59% of the total) are endemic to Costa Rica and Panama. Endemism is particularly high in Panama, where 38 taxa (34 species) of 81 (47%) are endemic. In Costa Rica 7 of 47 taxa (46 species) (15%) are endemic. Costa Rican endemics are: *P. aromaticum*, *P. auriculatum*, *P. chirripoense*, *P. cotobrusense*, *P. dominicalense*, *P. microstictum*, and *P. wilburii* var. *wilburii*. Mexico has a higher rate of endemism, with 7 of 21 (20 species) (33%) endemic. Mexican endemics are: *P. basii*, *P. breedlovei*, *P. dressleri*, *P. radiatum* var. *pseudoradiatum*, *P. hederaceum* var. *oxycardium*, *P. sousae*, and *P. subincisum*. In Middle America little endemism occurs. With the exception of Belize, which has one endemic (*P. dwyeri*), no other country in Middle America has any endemic species.

The distribution of Central American *Philodendron* reflects the trend for endemism in the genus. Only 27 species (28 taxa) (a total of 26% of all Central American species of *P.* subg. *Philodendron*) range into South America, eight (7% of the total) only to Colombia (Appendix 1). These are: *P. heleniae, P. immixtum, P. ligulatum* var. *ligulatum, P. malesevichiae, P. mexicanum, P. pseudauriculatum, P. radiatum* var. *radiatum,* and *P. squamicaule.*

Sixteen Central American taxa occur in Ecuador (Appendix 1), all but two (*P. brevispathum* and *P. jacquinii*), ranging along the Pacific slope of the Andes. These are: *P. brunneicaule, P. dodsonii, P. grandipes, P. hebetatum, P. platypetiolatum, P. purpureoviride, P. hederaceum* var. *kirkbridei, P. hederaceum* var. *hederaceum, P. squamipetiolatum, P. scalarinerve, P. squamicaule, P. tenue, P. tripartitum,* and *P. verrucosum.* Of these 14 taxa, 1, *P. hederaceum* var. *kirkbridei,* skips Colombia or has not yet been collected there. *Philodendron dodsonii* is particularly unusual in being absent from Panama.

Eight Central American species, *P. brevispathum, P. fragrantissimum, P. hederaceum, P. jacquinii, P. jodavisianum, P. sagittifolium, P. strictum,* and *P. tenue,* range to Venezuela. The ranges of *P. brevispathum, P. fragrantissimum,* and *P. hederaceum* also extend into the Amazon drainage, while the others occur either on the northern slope of the coastal cordillera or otherwise in the drainage of the Orinoco River Basin. Curiously only four species, *P. brevispathum, P. fragrantissimum, P. hederaceum,* and *P. verrucosum,* occur in the Amazon drainage. Three additional species, *P. jacquinii, P. strictum,* and *P. tenue,* occur east of the Andes, but only along the Cordillera de Mérida, the Cordillera de la Costa or the northern part of the Guiana Highlands and within the drainage of the Río Orinoco.

The only truly widespread Central American species of *P.* subg. *Philodendron* is *P. hederaceum,* which occurs virtually throughout the Neotropics, and is one of only two species (the other being *P. verrucosum*) that occurs on both slopes of the Andes. *Philodendron fragrantissimum* is probably the next most widespread species, ranging from Belize to the West Indies and into South America to the Guianas, northern Brazil, and to southern Peru.

Further collecting in Colombia, especially along the western slope of the Andes, will probably change these statistics but the figures most likely reflect the realities of life zone ecology and geologic history of the area rather than under-collecting. Since relatively few species of Araceae are known to occur at lower elevations on both the eastern and western side of the Andes, it can probably be presumed that the evolution of the respective Amazonian and Pacific coastal floras occurred independently after the Andes began to arise toward the end of the Cretaceous (Raven & Axelrod, 1974). The relatively few truly wide-ranging species, i.e., those ranging from Mexico to Brazil, appear to attest to this isolation. In Central America only one species, *P. hederaceum,* really falls into such a category, and it is also common in the West Indies indicating that it may have an ancient origin (or be easily dispersed). The high rates of endemism in Costa Rica, Panama, and Mexico perhaps reflect the isolation of these areas during periods when the oceans were at much higher levels than they are today and when the area that is now central Panama and Costa Rica was disconnected from South America. Much of the present area of Central America was submerged during early times. At the close of the Tertiary, 800,000 years ago, sea level was about 100 m higher than today (Holmes, 1969). The land mass of what is now Central America began to emerge as a series of islands during the Oligocene with further uplifting during the Middle Miocene. It was not until the Upper Miocene and Pliocene that the final portions of the isthmus of Panama emerged above sea level (Torre, 1965), and the final connection of Central and South America was made about 5.7 million years ago. In order to place these geological events in relation to the modern aroid flora, it should be noted that even during this era precursors to the existing flora probably already existed, since the angiosperm floras of the Oligocene were believed to have consisted almost entirely of existing genera, and the floras of the Oligocene and Pliocene probably already had existing species (Takhtajan, 1969).

Just as important as geology, from the standpoint of the isolation of the Central American aroid flora, are ecological factors that would cause Central American species to be isolated from those of South America. Much of eastern Panama consists of broad expanses of *Tropical moist forest* with other, generally smaller areas of *Premontane wet* and *Tropical wet forest.* In contrast to Panama, much of the area of northwestern Colombia in the Department of Chocó consists of much wetter pluvial forest with annual precipitation often exceeding 11,700 mm in some parts of the region (Gentry, 1982). This broad band of pluvial forest with its own suite of unique endemic species no doubt acts as a barrier for species from regions with lesser rainfall amounts. It probably also accounts for the Panamanian and Costa Rican species that skip the wettest areas of northwest South America but recur in the relatively drier areas of mesic western Ecuador.

Just as the Central American *P.* subg. *Philodendron* flora is rather isolated from that of South America, there is a certain amount of isolation within different parts of Central America. In comparison to Mexico and Costa Rica/Panama, Middle America (Appendix 1) has low species diversity, with Guatemala having only 15 species, Honduras 13 species, and Nicaragua 18. Most of the species in Honduras, excepting *P. anisotomum*, *P. mexicanum*, and *P. warszewiczii*, are shared with Nicaragua (see Appendix 1). Nicaragua has eight additional taxa not shared with Honduras: *P. brevispathum*, *P. grandipes*, *P. immixtum*, *P. ligulatum* var. *ligulatum*, *P. platypetiolatum*, *P. pterotum*, *P. tenue*, and *P. wendlandii*. All of the latter are shared with Costa Rica and Panama. Guatemala shares only about half of its species with Honduras and Nicaragua, namely *P. fragrantissimum*, *P. jacquinii*, *P. jodavisianum*, *P. radiatum*, *P. sagittifolium*, *P. smithii*, and *P. tripartitum*. Its other species are shared only with Mexico (or rarely with Costa Rica and Panama, e.g., *P. mexicanum*). These are: *P. advena*, *P. anisotomum*, *P. glanduliferum*, *P. mexicanum*, *P. purulhense*, *P. verapazense*, and *P. warszewiczii*.

The low species diversity and the very low endemism in Middle America are perhaps explained by the fact that Central America is rather more remote from existing large land masses to the north and the south, leaving it isolated from the independent evolution that must have been taking place in both of these larger areas (see below for a discussion of the possible origins of the respective species in Central American *Philodendron*). There is strong evidence, at least based on the distribution of modern aroid species, that the northwestern part of Middle America may have been isolated from Costa Rica by the San Juan Depression. Many of the species that occur in Costa Rica or Panama enter into Nicaragua in only a small area in the southeastern part of the country. Although the contemporary flora of Guatemala does not reflect isolation from Mexico to the same degree, it is possible that the more elevated portions of Guatemala, Nicaragua, and Honduras were isolated from major portions of Mexico at the Isthmus of Tehuantepec.

Certainly the Mexican aroid flora appears to be quite isolated, even when compared to the western parts of Middle America (here defined as Guatemala to Nicaragua). Mexico, in addition to having one-third of its species endemic, has relatively few species of *Philodendron* that range throughout Central America. Aside from the aforementioned *P. hederaceum*, only *P. jacquinii*, *P. jodavisianum*, *P. radiatum*, *P. sagittifolium*, and *P. tripartitum* range to northern South America. Two additional species, *P. anisotomum* and *P. mexicanum*, range as far as Panama. Several taxa, *P. advena*, *P. glanduliferum* var. *glanduliferum*, and *P. verapazense*, range only to Guatemala. *Philodendron purulhense* and *P. warszewiczii* range to Honduras, and *P. smithii* ranges to Nicaragua.

Taken together, Honduras and Nicaragua have 21 species of *Philodendron*. Of these, 8 species, *P. advena*, *P. anisotomum*, *P. mexicanum*, *P. radiatum*, *P. sagittifolium*, *P. smithii*, *P. tripartitum*, and *P. warszewiczii*, appear to be of Mexican origin, or in the case of the more widespread and variable species, namely *P. radiatum*, *P. sagittifolium*, and *P. tripartitum*, they may have originated in Panama or Costa Rica and ranged to both Mexico and South America. Certainly, in terms of morphological variation, all of these species are much more variable in Panama and Costa Rica than they are further north. *Philodendron jacquinii* has a circum-Caribbean distribution, indicating that it may be of West Indian origin. It is difficult to determine the origin of *P. hederaceum* given its extensive distribution. Three species, *P. brevispathum*, *P. fragrantissimum*, and *P. tenue*, probably originated in South America considering their widespread distribution there. *Philodendron platypetiolatum*, ranging from Ecuador and barely entering Nicaragua, may be another South American derivative. The remainder, *P. angustilobum*, *P. grandipes*, *P. immixtum*, *P. jodavisianum* (ranging barely to Chiapas and rare there), *P. ligulatum* var. *ligulatum*, *P. pterotum*, *P. rothschuhianum*, and *P. wendlandii*, are probably of Panamanian or perhaps Costa Rican origin.

The Costa Rican and Panamanian species not already discussed above appear not to have strong affinities with South American species, and clearly did not originate in areas of Middle America. Much of the flora of adjacent Nicaragua is closely related to that of Costa Rica. Except for those rather widespread species mentioned above, i.e., *P. brevispathum*, *P. fragrantissimum*, and *P. tenue*, as well as *P. platypetiolatum* (already discussed), there are relatively few species likely to be of South American origin. *Philodendron verrucosum* is almost certainly a South American species, since it is relatively widespread there, occurring on both sides of the Andes. In addition, it seems to have more related species in parts of South America especially in the Andes of western Colombia.

Philodendron dodsonii, which occurs in Ecuador but not Colombia, is just as likely to have originated in South America as in Central America. The same is true of *P. strictum*, which is known from eastern Venezuela and has relatives in the Andes of central Colombia, as well as *P. hebetatum*, which

is rather widespread in western South America as far south as Ecuador. Moreover, the latter apparently does not even reach Costa Rica, making the case for a South American origin even more likely.

Philodendron grandipes, known from western South America as far south as Ecuador, might conceivably be of South American origin despite being very widespread and common as far north as Nicaragua. More probably of South American origin is *P. heleniae*, which is common in Colombia and ranges only to western Panama. Moreover, it seems to have a close relative on the eastern slopes of the Andes.

Three species with scaly parts, *P. malesevichiae*, *P. squamicaule*, and *P. squamipetiolatum*, are moderately rare in Panama, and though all are still poorly known in Colombia, they are more likely to have originated in northwestern Colombia where there are several other relatives with scaly parts.

Some taxa, such as *P. ligulatum* var. *ligulatum*, *P. pseudauriculatum*, and *P. scalarinerve*, either barely enter Colombia or are rare there and are more likely therefore to have originated in Central America. All the remaining species of *P.* subg. *Philodendron* occur in Panama or Costa Rica, with 11 species shared between the two countries.

Taxonomic Treatment

Philodendron ("Philodendrum") Schott, Wiener Z. Kunst. 1829: 780. 1829, nom. et orth. cons. TYPE: *P. grandifolium* (Jacq.) Schott (*Arum grandifolium* Jacq.)

Telipodus Raf., Fl. tellur. 3: 66. 1836[1837]. TYPE: *T. grandifolium* (Jacq.) Raf. (*Arum grandifolium* Jacq.)

Thaumatophyllum Schott, Bonplandia 7: 31. 1859. TYPE: *T. spruceanum* Schott

Elopium H. W. Schott, Oesterr. Bot. Z. 15: 34. 1865. TYPE: *E. surinamense* (Miq.) Schott (*Anthurium surinamense* Miq.)

Baursia T. Post & Kuntze, Lex. gen. phan. 62. 1903. TYPE: *Caladium bauersii* Rchb.

Appressed-climbing or scandent hemiepiphytes, sometimes epiphytes or terrestrial herbs (sometimes stout and arborescent); growth sympodial, anisophyllous, or (more commmonly) diphyllous; trichoschlereids absent, biforines and secretion files present. Leaves with spiral phyllotaxy; petioles rarely geniculate, sheath obsolete or extensive; blades with parallel-pinnate venation, hypostomatic with stomates paracytic, simple to trifoliolate, pinnatifid, bipinnatifid, or (rarely) pedately compound. Inflorescence terminal (appearing axillary), solitary to multiple in leaf axils; spathe enveloping the spadix and constricted or not, usually persistent: spadix monoecious, with sterile male flowers below or both below and (rarely) above the fertile male region; flowers naked, unisexual. Male flowers with 2–6 free stamens, connective enlarged; anther dehiscence by apical slits or pores; pollen inaperturate, boat-shaped, subisopolar, bilaterally symmetrical, shed in monads, medium-sized (mean 40 μm; range 28–54 μm), the exine coarsely verrucate to subfoveolate or (most frequently) psilate; pollen at anthesis binucleate and starch-bearing. Female flowers virtually always lacking staminodes, ovary (2–3)4–6(47)-locular, each locule with axile or (rarely) basal placentation and (1–)4–51 or more orthotropous or hemiantropous, endospermous ovules. Fruit a berry, usually white or orange. Chromosome numbers $2n = 30, 32, 34, 36$. [Description adapted from Grayum (1996).]

Key to *Philodendron* Subgenera

1a. Stem of mature flowering plants with a succession of many leaves terminated by solitary or paired (rarely 3) inflorescences; petioles with long sheaths narrowly encircling the stem at base, winged to at least midway on adult plants; up to 5 leaves produced on the stem between each successive inflorescence ..... subg. *Pteromischum*

1b. Stem of mature flowering plants with a succession of short sympodial segments each bearing a cataphyll and a single leaf with the inflorescence(s) 1 to 10 and appearing to be borne in the leaf axils; petioles of leaves of adult plants with a short, usually inconspicuous petiole sheath borne on the side of the stem, not encircling it at the base (sometimes fully winged on juvenile plants); inflorescences produced with each new leaf (though frequently aborted).

2a. Stems often arborescent, with conspicuous leaf scars and frequently interpetiolar scales persisting around at least the upper margins of the petiolar scars; male flowers conspicuously elongate, up to 10 times longer than wide; staminodial zone between staminate and pistillate zones of the spadix subequal or longer than fertile zone ..... subg. *Meconostigma*

2b. Stems rarely arborescent, often scandent, stout or slender and with interpetiolar scales lacking; male flowers only 2–3 times longer than wide; staminodial zone between staminate and pistillate zones of spadix much shorter than the fertile staminate zone ..... subg. *Philodendron*

Philodendron subg. **Philodendron** Schott. *Philodendron* subg. *Euphilodendron* Engl., Bot. Jahrb. Syst. 26: 509. 1899. *Baursia* subg. *Eubaursia* Kuntze in T. Post & Kuntze, Lex. gen. phan. 62.

Appressed hemiepiphytic climbers or vines with aerial roots, less frequently terrestrial with creeping rhizomatous or deeply rooted stems, rarely short-

stemmed true epiphytes, rarely somewhat arborescent in Central America; sometimes with flagelliform shoots; sap usually tanniniferous and drying dark, rarely with latex and drying white; stems of monophyllous sympodia with elongated hypopodial internodes, densely rooted at nodes; internodes often much longer than broad or about as long as broad, sometimes broader than long at anthesis, sometimes flattened on one side, often coarsely pale-streaked just below the node, usually green and semiglossy, but often turning gray-green to brownish or reddish brown in age; juvenile plants terrestrial or epiphytic and scandent, the petioles conspicuously sheathed and subtended by inconspicuous intravaginal squamulae; cataphylls of mature stems unribbed or variously ribbed, caducous, marcescent and deciduous or persistent and membranaceous to moderately coriaceous, remaining intact or more commonly decomposing to net-like, persistent fibrous reticulum. Leaves usually long-petiolate; petioles usually with ligulate sheath in juvenile plants, on adult plants usually sheathed only at base, variously shaped in cross section, firm or spongy, usually smooth, frequently densely pale-short-lineate or pale-striate throughout, sometimes warty or covered with scale-like processes, rarely geniculate apically; blades simple and entire, ovate, cordate, hastate, sagittate, oblong to elliptic or variously divided, trifid, trifoliolate, or pinnatifid; midrib raised or sunken above, raised below; primary lateral veins pinnate, usually conspicuous, spreading to the margins and running into an antemarginal collective vein; lowermost primary lateral veins (basal veins) often coalesced on cordate blades, the posterior rib (coalesced basal veins) naked along the sinus or not; interprimary veins sometimes present; secondary lateral and higher order veins transversely reticulate between the secondary veins, sometimes all veins slender with no distinct primary lateral veins; minor veins conspicuous or obscure, usually fine and closely parallel; crossveins (minute veins extending transversely between the minor veins) sometimes visible; secretory ducts sometimes appearing like veins, linear, short to long, obscure to very distinct on lower surface. Inflorescences 1–several per axil, usually much shorter than the petioles; peduncles shorter or longer than the spathe; spathe erect, usually coriaceous, entirely persistent, often with large superficial resin canals on inner surface which exude resin, opening widely at anthesis (usually for about one day), then reclosing and persisting in fruit, deciduous only on ripening of fruit, frequently colorful, often bicolorous on outside, typically somewhat constricted between tube and blade, convolute at base; tube cylindric to inflated, uniformly greenish to red or violet-purple within; blade usually opening widely, becoming ± boat-shaped at anthesis, usually white within, sometimes tinged reddish; spadix sessile to stipitate, divided into pistillate and staminate portions, each with unisexual flowers; pistillate zone usually greenish, obliquely fused at its base to the spathe, free above, usually much shorter than the staminate portion and separated from it by a sterile zone of staminodial flowers; intermediate sterile zone cylindric to ellipsoid, much shorter than staminate zone in Central America, usually thicker than staminate zone; staminate zone terete to clavate, white, usually somewhat constricted above the sterile staminate zone; flowers unisexual, naked, closely aggregated in several spirals; staminate flowers 2–6(usually 4–5)-androus; stamens free, adjacent, lacking stomial groove, prismatic to obpyramidal; anthers tetrasporangiate (with microsporangia embedded in the abaxial surface of the anther), columnar in shape, elliptic, ovate to rhombic in cross section, sessile to subsessile; connective thick, apically truncate, usually irregularly 4–5-sided, overtopping thecae; thecae oblong or elliptic, emarginate at the base, dehiscing apically by short, ragged lateral pores; endothecial thickenings lacking; pollen extruded in strands or mixed with resin secretion or exuded in amorphous masses, inaperturate, ellipsoid or oblong or occasionally elongate, medium sized (mean 40 μm, range 28–54 μm), mostly perfectly psilate, sometimes minutely verruculate, scabrate or fossulate to clearly punctate, subfossulate, subfoveolate or subverrucate; sterile staminate flowers naked, usually prismatic, truncate and usually more irregular than fertile flowers and lacking thecae; pistillate flowers with ovary syncarpous, ovoid, subcylindric, cylindric or obovoid, 3–9(14)-locular in Central America (2-locular in *P.* sect. *Philopsammos* in South America); carpels presumably equal to number of locules; placentation axile, sub-basal or basal; ovules 1 to numerous (to ca. 30) per locule, usually hemiorthotropous, rarely hemianatropous, ascending on moderately long or sometimes short funicles; stylar region as broad as or sometimes slightly narrower than ovary; style short, unlobed, with or without boss (see definition under Style Type D), funnel, or annulus; central style dome usually lacking in Central America; stigma sessile, hemispherical to lobulate. Berries subcylindrical to obovoid, exposed by the re-opening of the spathe, white, whitish translucent to red or orange; seeds few to many per berry, oblong to ellipsoid or ovoid-oblong, testa rather thick, striate-costate, rarely sarcotestate; embryo axile, straight, elongate, endosperm copious; chromosomes: $2n = 30, 32, 34, 36, (26, 48)$. Species ca. 700, Central Mexico to Argentina; West Indies (occurring in all countries of Central and South America except Chile and Uruguay).

KEY 1: BLADES DEEPLY LOBED OR DIVIDED 382

KEY 2: BLADES SIMPLE, NON-CORDATE, EITHER OBLONG OR OVATE; SOMETIMES SUBCORDATE TO CORDULATE AT BASE, THE POSTERIOR LOBES UP TO ¼ AS LONG AS ANTERIOR LOBES 383

KEY 3: CORDATE BLADES WITH PERSISTENT CATAPHYLLS 385

KEY 4: VINES WITH CORDATE BLADES AND DECIDUOUS CATAPHYLLS 388

KEY TO *PHILODENDRON* SUBGENUS *PHILODENDRON* OF CENTRAL AMERICA

A. Blades deeply divided, either pinnately lobed, or 3-lobed to trifoliate ..... **KEY 1**
A′. Blades not deeply divided, at most with the margins merely sinuate, the lateral margins of the anterior lobe sometimes deeply concave, but not to such an extent that the blade looks decidedly 3-lobed (blades at first entire, but naturally splitting into irregular segments in *P. findens*).
  B. Blades acute, obtuse or truncate at base or sometimes weakly cordulate or subcordate but with the posterior lobes only ¼ as long as the anterior lobe or less ..... **KEY 2**
  B′. Blades cordate, sagittate, or hastate at base, the posterior lobes usually more than ¼ as long as the anterior lobes.
    C. Cataphylls persistent on stem, either intact or as fibers ..... **KEY 3**
    C′. Cataphylls ultimately deciduous, though sometimes persisting ..... **KEY 4**

KEY 1: BLADES DEEPLY LOBED OR DIVIDED

1a. Blades deeply pinnnately lobed, the divisions extending at least ¼ of the way to the midrib.
  2a. Leaves bipinnately lobed, the blade divisions near the middle of the blade pinnately lobed, usually divided more than ½-way to the midrib.
    3a. Blades lobed only $^{3}/_{10}$–$^{7}/_{10}$ the way to the midrib; Mexico (Sinaloa & Nayarit); 0–370 m ..... *P. dressleri* G. S. Bunting
    3b. Blade deeply lobed, the divisions extending more than $^{7}/_{10}$ of the way to the midrib.
      4a. Blades deciduous during the dry season; leaf segments thin, drying papyraceous, pale yellow-green to yellow-brown, with the minor veins distinctly visible and darker than surface; lateral segments with usually 3 or more lobes per side, extending to below the middle of the pinnae; Mexico (Jalisco & Chiapas) to El Salvador, Guatemala, Honduras, and Nicaragua, 300–1500 m ..... *P. warszewiczii* K. Koch & Bouché
      4b. Blades evergreen; leaf blade segments subcoriaceous, drying moderately thick, dark brown or sometimes reddish brown, the minor veins not distinctly visible on drying, not markedly darker than surface; lateral segments with usually 1–2 lobes per side, usually restricted to near the apex of the pinnae; Mexico to Colombia, 0–700, rarely to 1860 m ..... *P. radiatum* var. *radiatum*
  2b. Leaves merely pinnately lobed, the blade divisions near the middle of the blade not pinnately lobed, or, if so, divided less than ½-way to the midrib ..... *P. radiatum* var. *pseudoradiatum* Croat
1b. Blades deeply 3-lobed or trifoliate.
  5a. Blade with the medial lobe less than 1.7 times longer than the lateral lobes; lateral lobes directed ± toward the apex.
    6a. Lateral lobes of the blade broadly confluent with the medial lobe by at least 2 cm from the base of the blade (as measured from the depths of the incised area and the apex of the petiole); inflorescences usually 3–9 per axil.
      7a. Medial lobe of the blade with 5–12 pairs of primary lateral veins; spathe tube uniformly greenish to whitish within; Honduras to Panama, usually below 1000 m ..... *P. rothschuhianum* (Engl.) Croat & Grayum
      7b. Medial lobe of the blade with 18–19 pairs of primary lateral veins; spathe tube red-violet or purplish within; Costa Rica (Puntarenas, San José), 1000–1250 m ..... *P. cotobrusense* Croat & Grayum
    6b. Lateral lobes of the blade not confluent with or only weakly confluent with the medial lobe to no more than 1 cm from the base of the blade; inflorescences usually 1, rarely to 3 per axil.
      8a. Medial lobe of blades with more than 18 pairs of primary lateral veins, elliptic; central Panama, 350–450 m ..... *P. madronense* Croat
      8b. Medial lobe of blade with fewer than 12 pairs of primary lateral veins, usually oblanceolate to oblong-lanceolate; widespread species, Mexico to Ecuador.
        9a. Medial lobe mostly 3–3.5 times longer than broad (rarely as little as 1.7 times longer than broad); primary lateral veins of medial lobe 4–12 per side, prominently sunken; lateral lobes directed ± toward the apex; minor veins arising from both the midrib and the primary lateral veins; ripe fruits whitish; Mexico to Ecuador, 0–1300(1500) m ..... *P. tripartitum* (Jacq.) Schott
        9b. Medial lobe mostly 1.5–2 times longer than broad; primary lateral veins of medial lobe mostly 2–4, rarely 5 per side, weakly sunken; lateral lobes directed ± outward; minor veins arising only from the midrib; ripe fruits orange; Mexico to Costa Rica, 30–1800 m ..... *P. anisotomum* Schott

5b. Blades with the medial lobe more than 1.7 times longer than the lateral lobes; lateral lobes directed laterally (spreading) outward or even downward toward the base of the petiole (reflexed).
10a. Blades sagittate, the lateral lobes directed downward somewhat toward the base of blade (in direction of petiole); Mexico to Panama and South America, 0–1900 m ..... *P. mexicanum* Engl.
10b. Blades hastate, the lateral lobes directed outward at ca. 90° angle.
11a. Lateral lobes confluent with the medial lobe by usually for more than 4 cm (rarely to 3.3 cm); basal veins 8–10 per side; Honduras to Panama, 0–680 m ..... *P. angustilobum* Croat & Grayum
11b. Lateral lobes confluent with the medial lobe by usually less than 3 cm (rarely to 8 cm); basal veins 4–7 per side; Mexico to Costa Rica, 30–1800 m ..... *P. anisotomum* Schott

KEY 2: BLADES ENTIRE OR SHALLOWLY DIVIDED, NON-CORDATE, EITHER OBLONG OR OVATE; SOMETIMES SUBCORDATE OR CORDULATE AT BASE, THE POSTERIOR LOBES UP TO ¼ AS LONG AS ANTERIOR LOBES

1a. Plants vines or at least with internodes much longer than broad.

VINES OR SCANDENT: INTERNODES MUCH LONGER THAN BROAD; BLADES OVATE

2a. Blades ± ovate, less than 2 times longer than wide.
3a. Blades with primary lateral veins either 2 or fewer or with the primary lateral veins inconspicuous, scarcely more distinct than the minor veins.
4a. Blades more than 11 cm wide; peduncles more than 10 cm long; Costa Rica, 50–450 m ..... *P. microstictum* Standl. & L. O. Williams
4b. Blades less than 11 cm wide; peduncles less than 10 cm long.
5a. Internodes less than 10 cm long; blades less than 1.4 times longer than wide, drying greenish, lacking primary lateral veins; Panama, Cerro Brewster, 850 m ..... *P. brewsterense* Croat
5b. Internodes more than 10 cm long; blades ca. 2 times longer than wide, drying brown, with up to 2 obscure primary lateral veins; Costa Rica, Río Chirripó del Pacífico, San José Prov., 1000 m ..... *P. chirripoense* Croat & Grayum
3b. Blades with the primary lateral veins more than 2 and much more prominent than the minor veins.
6a. Blades ovate to broadly ovate, mostly less than 1.7 times longer than wide.
7a. Stems, petioles, and inflorescences densely scaly (petiolar scales slender and spreading); major veins on lower surface densely puberulent; Panama to Ecuador, 0–1300 m ..... *P. squamipetiolatum* Croat
7b. Stems, petioles, and inflorescences glabrous; major veins on lower surface glabrous; Panama (Coclé, Veraguas), 770–1200 m ..... *P. ligulatum* var. *ovatum* Croat
6b. Blades narrowly ovate to oblong-elliptic, usually more than 2 times longer than wide.
8a. Blades less than 12 cm wide; posterior lobes about as long as broad; Panama to Colombia, 0–140 m ..... *P. immixtum* Croat
8b. Blades usually more than 12 cm wide; posterior lobes much broader than long; Costa Rica to Panama, (210)670–1800 m ..... *P. lentii* Croat & Grayum
2b. Blades ± oblong to oblong-elliptic (rarely narrowly ovate) or oblanceolate, usually more than 2.5 times longer than wide.

VINES WITH ± OBLONG BLADES

9a. Blades lacking distinct primary veins at base of blade; primary lateral veins obscure or lacking.
10a. Blades drying gray-green; primary lateral veins not at all apparent; Panama (San Blas), near sea level ..... *P. ubigantupense* Croat
10b. Blades drying reddish brown or blackened; primary lateral veins 3–6, obscure but still visible.
11a. Blades drying blackened, usually more than 25 cm long; spathe more than 12 cm long; Panama (Bocas del Toro and Chiriquí), 780–1400 m ..... *P. correae* Croat
11b. Blades drying reddish brown, usually less than 25 cm long; spathe less than 12 cm long; Costa Rica (100–900 m) to Panama, 900–1420 m ..... *P. bakeri* Croat & Grayum
9b. Blades with one or more distinct primary veins at base of blade; primary lateral veins distinct.
12a. Petioles encircled distally with a dark purplish (or dark green) ring separating the petiole and the blade.
13a. Blades with posterior lobes usually narrowly rounded and somewhat spreading or broader than long, rarely about as long as broad; inflorescences 1–3 per axil; Panama, 100–970 m ..... *P. annulatum* Croat
13b. Blades with posterior lobes about as broad as long and held closely near the petiole; inflorescence usually solitary (sometimes 2 in *P. immixtum*).
14a. Blades typically drying greenish to greenish brown, rarely more than 30 cm long; Panama to Colombia, 0–140 m ..... *P. immixtum* Croat
14b. Blades typically drying blackened, rarely less than 30 cm long; Nicaragua to Colombia, 0–1200 m ..... *P. ligulatum* Schott var. *ligulatum*
12b. Petioles lacking a dark purple distal ring.

15a. Blades less than 10 cm wide; stem minutely pale granular-puberulent at high magnification; pistil with a funnel-shaped stigma (type E); ovules 1 per locule; Panama (Darién), 75 m ..... *P. granulare* Croat

15b. Blades usually more than 15 cm wide (rarely to as little as 10 cm wide in *P. heleniae*); stems smooth to irregularly ridged or folded at high magnification (sometimes minutely warty but not pale granular-puberulent); pistil with a flat style apex (type B); ovules 3 or more per locule.

16a. Blades drying coriaceous, lacking secretory ducts; spathes greenish white to white outside, more than 10 cm long; Costa Rica to Panama, (210)670–1800 m ..... *P. lentii* Croat & Grayum

16b. Blades drying subcoriaceous, with conspicuous secretory ducts; spathes red outside, mostly less than 10 cm long; Panama and Ecuador, mostly 100–1040 m ..... *P. heleniae* Croat

1b. Plants appressed-climbing or sometimes terrestrial, with the internodes typically broader than long or only slightly longer than broad.

NON-VINING PLANTS; BLADES OBLONG

17a. Cataphylls deciduous.

18a. Blades usually prominently lobed at base, the lobes typically longer than broad or at least usually spreading away from the petiole.

19a. Blades thin-drying; sinus arcuate with blade tissue somewhat decurrent on petiole; petiole drying 2–4 mm diam.; Panama, E of Canal Area, 450–850 m ..... *P. morii* Croat

19b. Blades thick-drying; sinus oblong to parabolic or arcuate but with blade tissue not at all decurrent onto petiole; Panama, 100–970 m ..... *P. annulatum* Croat

18b. Blades not lobed at base or merely cordulate with posterior lobes round, as broad as long, held closely against the petioles.

20a. Largest leaf blades more than 50 cm long.

21a. Blades usually more than 30 cm wide; petioles usually about 85% the length of the blades or even longer than the blades; Costa Rica and Panama, 0–200 m ..... *P. davidsonii* Croat

21b. Blades less than 30 cm wide; petioles typically much shorter than the blade.

22a. Blades drying reddish brown, 4.4–4.9 times longer than wide; petioles lacking a purple distal ring; Panama, 325–650 m ..... *P. dolichophyllum* Croat

22b. Blades drying dark gray-green to blackened, usually less than 4.3 times longer than wide; petiole with a purple or green distal ring.

23a. Petioles subterete adaxially, not at all winged marginally; Panama and Colombia, 20–1400 m ..... *P. pseudauriculatum* Croat

23b. Petioles sharply D-shaped with slender wings on the adaxial margins; Panama, Darién, 50–200 m ..... *P. ligulatum* var. *heraclioanum* Croat

20b. Largest leaf blades usually less than 50 cm long.

24a. Blades usually drying green to yellowish green, thin.

25a. Blades oblong-lanceolate, less than 7 cm wide, obtuse to almost rounded at base and then decurrent along petiole; Panama (Coclé), 700–800 m ..... *P. folsomii* Croat

25b. Blades ovate-triangular, 11–16 cm wide, subcordate at base; eastern Panama, 450–850 m ..... *P. morii* Croat

24b. Blades drying yellow-brown or brownish, gray-brown to reddish brown, moderately coriaceous.

26a. Inflorescences 2–10 per axil; peduncle less than 6 cm long; spathe tube reddish maroon outside and within; leaf blades with conspicuous secretory ducts visible on the lower dried surface; Panama to Colombia and Ecuador, 20–1040(1450) m ..... *P. heleniae* Croat

26b. Inflorescence solitary; peduncle ca. 9 cm long; spathe tube green outside, white within; leaf blades lacking any sign of secretory ducts; Panama (Colón), ca. 200 m ..... *P. utleyanum* Croat

17b. Cataphylls persistent.

27a. Plants usually terrestrial and rosulate; petioles deeper than wide; blades usually elliptic to oblong-elliptic, acute to narrowly rounded at base; Panama to Colombia, 100–1000 m ..... *P. roseospathum* Croat

27b. Plants epiphytic to hemiepiphytic, not rosulate; petioles as deep as wide; blades linear to oblanceolate or oblong-elliptic, sometimes weakly cordate to cordulate at base.

28a. Blades linear to oblanceolate, attenuate at base; primary lateral veins arising at 25–45° angle from midrib; cross-veins not visible on drying; sap chalky white; Costa Rica to Panama, 0–900 m ..... *P. cretosum* Croat & Grayum

28b. Blades oblong-elliptic to narrowly ovate, obtuse to subcordate at base; primary lateral veins arising at 60–75° angle; cross-veins very conspicuous on drying; sap not colored, or if so not white; Costa Rica to Colombia, 0–1325 m ..... *P. scalarinerve* Croat & Grayum

29a. Blades usually broadest above the middle, acute, obtuse, narrowly rounded to merely minutely cordulate at base.

30a. Petioles sharply flattened adaxially (with acute lateral margins); blades acute to narrowly rounded (never cordulate) at base, mostly more than 2.5 times longer

than petioles; internodes broader than long; Costa Rica, Nicaragua, and Panama, Atlantic slope; 10–1250 m ..... *P. wendlandii* Schott

30b. Petioles subterete; blades narrowly cordulate at base, less than 1.8 times longer than petioles; internodes often longer than broad; southwestern Costa Rica, Pacific lowlands, 0–1200 m ..... *P. auriculatum* Standl. & L. O. Williams

29b. Blades broadest below the middle, cordate to subcordate at base (acute to truncate in *P. davidsonii* subsp. *bocatoranum*).

31a. Blades ovate to broadly ovate, less than 60 cm long, drying dark brown; primary lateral veins 5–9 per side; petioles terete; Panama (Darién), ca. 1500 m ..... *P. niqueanum* Croat

31b. Blades ovate-oblong, usually more than 60 cm long, drying light brown; primary lateral veins 18–21 per side; petioles thicker than broad (i.e., with the thickest dimension perpendicular to the plane of the blade) and broadly sulcate adaxially; Costa Rica to Panama, 0–200 m ..... *P. davidsonii* Croat

KEY 3: CORDATE BLADES WITH PERSISTENT CATAPHYLLS

1a. Blades with posterior rib (union of basal veins) naked along the edge of the sinus.

2a. Petioles with conspicuous, elongate, hair-like scales.

3a. Petiolar scales scattered and mostly in the distal ½ of petiole; plants terrestrial; Panama and Colombia, 830–860 m in Panama, 50–150 m in Colombia ..... *P. malesevichiae* Croat

3b. Petiole scales dense, covering the entire petiole; plants usually hemiepiphytic.

4a. Blades ovate-triangular, typically more than 1.3 times longer than broad, semiglossy above, paler and solid light green to silvery-green beneath, Costa Rica to Ecuador, <100–1250 m ..... *P. squamicaule* Croat & Grayum

4b. Blades ovate, typically less than 1.3 times longer than broad, matte and subvelvety above, paler and tinged with purplish violet between the major veins below; Costa Rica to Peru, (200)500–1500 m ..... *P. verrucosum* L. Mathieu ex Schott

2b. Petioles glabrous or least lacking scales.

5a. Petioles conspicuously and sharply flattened adaxially, with lateral margins sharply edged or with a slender wing.

6a. Petioles merely sharply edged, lacking an actual wing at the margin.

7a. Blades whitish and matte below; cataphylls persisting in semi-intact fragments of thin epidermis; spathe tube green outside, at most tinged pink within; Costa Rica to Panama (Chiriquí), (775)1000–2100 m ..... *P. thalassicum* Croat & Grayum

7b. Blades green and semiglossy below; cataphylls persisting in a dense reddish brown, semi-intact mass; spathe tube green or bright red outside, dark red to maroon within, blade white; Belize to South America, 0–900 m.

8a. Blades ovate-triangular, 1.8–2.7 times longer than wide; cross-veins conspicuous between minor veins on dried blades; spathe tube green on outside; W Panama (Bocas del Toro to Coclé), 590–1300 m ..... *P. copense* Croat

8b. Blades mostly ovate, 1.1–1.7 times longer than wide; cross-veins between minor veins not at all apparent; spathe tube bright red outside; Belize to South America, 0–1000 m ..... *P. fragrantissimum* (Hook.) G. Don

6b. Petioles with a narrow marginal wing.

9a. Leaf blades promptly splitting into slender segments laterally, drying blackened; petiole wing undulate distally; Costa Rica to Panama, Atlantic slope, 0–1400 m ..... *P. findens* Croat & Grayum

9b. Leaf blades remaining intact, drying yellow-green; petiole wing usually undulate throughout its entire length; Nicaragua to central Panama, mostly less than 700 m ..... *P. pterotum* K. Koch & Augustin

5b. Petioles terete to obtusely flattened or U-shaped but not sharply flattened adaxially, if sulcate adaxially the margins merely obtuse.

10a. Blades whitish and matte on lower surface even on fresh leaves; petioles usually drying light yellowish brown (except sometimes not in *P. strictum*).

11a. Blades narrowly ovate, usually more than 1.8 times longer than wide; plants commonly hemiepiphytes; Panama to Ecuador, usually <1400 m ..... *P. hebetatum* Croat

11b. Blades ovate to broadly ovate, averaging 1.3 times longer than wide; typically terrestrial; Costa Rica to western Panama, Colombia, and Venezuela, mostly at 850–1665 m in Central America ..... *P. strictum* G. S. Bunting

10b. Blades green to yellow-green beneath, usually semiglossy to glossy; petioles drying various colors, not light yellowish brown (except *P. copense*, *P. schottianum*, and *P. thalassicum*).

NARROWLY OVATE BLADES

12a. Blades usually 1.8 times or more longer than wide.

13a. Spathe tube greenish to yellow-green or whitish inside.

14a. Leaf blades with lower surface matte, frequently bluish green; style apex prolonged into a short but distinct neck (style type D); central Costa Rica to western Panama, (775)1000–2100 m ..... *P. thalassicum* Croat & Grayum

14b. Leaf blades with lower surface glossy to semiglossy, not at all bluish green; style apex flat, not prolonged into a distinct neck (style type B; rarely type C); Panama, except *P. jodavisianum* (Mexico to Venezuela).
15a. Blades drying yellow-green; basal veins fewer than 5; sap milky white, drying chalky; inflorescence solitary; cataphylls to 40 cm long; Panama (Darién), 800–1480 m ..... *P. albisuccus* Croat
15b. Blades drying dark gray-brown to olive-green, typically somewhat blackened; basal veins usually more than 5; sap usually clear, drying dark brown to reddish; inflorescences 2–6 per axil; cataphylls less than 20 cm long.
16a. Petioles terete to obtusely flattened adaxially, lacking prominently raised lateral margins; peduncles frequently longer than the spathe; central and eastern Panama, 0–800 m ..... *P. panamense* K. Krause
16b. Petioles usually D-shaped or U-shaped, usually flattened adaxially with prominently raised margins, often thicker than broad, rarely C-shaped to subterete; peduncles usually much shorter than the spathe; S Mexico to Panama and Venezuela (Mérida), 0–1500 m ..... *P. jodavisianum* G. S. Bunting
13b. Spathe tube red to maroon or violet-purple on inside.
17a. Blades drying greenish to yellow-green (sometimes yellow-brownish in *P. alticola*), lacking conspicuous cross-veins.
18a. Pistils with 1 ovule per locule; leaf blades with secretory ducts moderately obscure, the abaxial surface densely and minutely granular on drying; staminate portion of the spadix constricted above the sterile portion, the fertile portion clavate, the sterile staminate portion only slightly thicker than the pistillate portion; dried style base doughnut-shaped with stylar canals at the bottom of a deep concavity; Panama (Chiriquí to Coclé, (750) 950–2200 m) and Costa Rica ..... *P. straminicaule* Croat
18b. Pistils with 12–18 ovules per locule; leaf blades with secretory ducts conspicuous, abaxial surface smooth on drying; staminate portion of the spadix scarcely constricted above the sterile portion, the fertile portion stubby and evenly tapered to the apex, the sterile staminate portion much thicker than the pistillate (approximately ½ thicker); dried style base raised but flattened at apex with a narrow pale ring around its outer margin, the stylar canals exserted like minute funnels and extending above the surface; eastern Costa Rica and western Panama, 800–2500 m ..... *P. alticola* Croat & Grayum
17b. Blades drying reddish brown with conspicuous cross-veins.
19a. Petioles drying with a conspicuous light reddish brown or yellow-brown epidermis, this smooth and often flaking; cataphylls less than 25 cm long; primary lateral veins 11–16 per side; basal veins frequently more than 8 per side; Panama (Bocas del Toro and Coclé Provinces), 590–930 m ..... *P. copense* Croat
19b. Petioles drying dark brown, the epidermis not peeling; cataphylls more than 55 cm long; primary lateral veins fewer than 8 per side; basal veins up to 8 per side; Panama (Chiriquí, Bocas del Toro, Coclé, and Veraguas Provinces), 500–1630 m ..... *P. chiriquense* Croat

OVATE TO BROADLY OVATE BLADES

12b. Blades usually about 1.5 times longer than wide or less (sometimes wider than long).
20a. Leaf blades with lower surface matte (but never velvety), frequently bluish green, the dried waxy surface forming an areolate pattern; central Costa Rica to western Panama, (775)1000–2100 m ..... *P. thalassicum* Croat & Grayum
20b. Leaf blades with lower surface semiglossy (or, if matte, then velvety), never bluish green.
21a. Leaf blades matte and velvety above; central Panama in the region of the isthmus, 300–375 m ..... *P. gigas* Croat
21b. Leaf blades semiglossy to glossy above.
22a. Peduncles usually less than 10 cm long (rarely longer in fruiting peduncles of *P. llanoense* and *P. dodsonii*).
23a. Spathe tube solid bright red on outside; central Panama (Veraguas and Coclé), 800–1200 m ..... *P. antonioanum* Croat
23b. Spathe tube green outside (sometimes tinged weakly red on *P. schottianum*).
24a. Spathe weakly or not at all constricted above the tube.
25a. Cataphylls persisting usually with large fragments of glossy, yellowish epidermis; petioles drying yellowish to yellowish brown and glossy as if with a layer of shellac; Costa Rica to Panama, 600–2200 m ..... *P. schottianum* H. Wendl. ex Schott
25b. Cataphylls persisting semi-intact and brown, not glossy or yellowish; petioles usually drying brown to blackened, usually not yellowish and glossy; Guatemala, 1360–1870 m ..... *P. purulhense* Croat
24b. Spathe moderately to prominently constricted above the tube.
26a. Leaf blades drying yellow-brown below, coriaceous; ovules mostly (6)12–(20) per locule; Isthmus of Panama, mostly below 500 m ..... *P. llanense* Croat

26b. Leaf blades drying reddish brown, moderately thin; ovules 1–6 per locule (except *P. dodsonii* with ca. 20 ovules per locule); Costa Rica or Mexico.

27a. Stems usually growing over rocks in dry habitats, rarely on trees; cataphylls eventually deciduous, intact on the older stem; ovules 4–6 per locule; western Mexico (Jalisco & Guerrero), 350–1250 m ..... *P. basii* Matuda

27b. Stems appressed-climbing on trees in humid habitats; cataphylls decomposing and breaking up before falling off; ovules either solitary or ca. 20 per locule; Costa Rica and/or Ecuador.

28a. Spathe tube green; ovules 1 per locule; posterior rib barely or not at all naked along the sinus (up to at most 2.5 cm); southwestern Costa Rica, 1000 m ..... *P. dominicalense* Croat & Grayum

28b. Spathe tube dark reddish to red-purple; ovules ca. 20 per locule; posterior rib naked to ca. 6 cm along the sinus; Costa Rica, principally on the Atlantic slope at 300–850 m and Colombia and Ecuador at 200–1300 m ..... *P. dodsonii* Croat & Grayum

22b. Peduncles usually more than 10 cm long (rarely less than 10 cm long) when not at anthesis.

29a. Stems clothed with a dense series of overlapping cataphylls, each persisting as a reticulum of coarse fibers often overlain with a thin, fragmented epidermis.

30a. Blades 1.2–1.5 times longer than wide, drying reddish brown above; Panama (Darién), 1000–1560 m ..... *P. pirrense* Croat

30b. Blades 0.8–1.4 times longer than wide, drying grayish green above.

31a. Dried blades with lower surface semiglossy, sparsely granular, with moderately conspicuous cross-veins, not speckled, the upper surface lacking raphide cells; ovules 6 per locule; Panama, Panama Province (Cerro Jefe), 550–800 m ..... *P. jefense* Croat

31b. Dried blades with lower surface matte, smooth and minutely brownish to whitish speckled, lacking obvious cross-veins, the upper surface usually with short whitish raphide cells visible; ovules 14–20 per locule; Panama, Canal Area to Darién Province (Cerro Sapo), 140–800 m ..... *P. lazorii* Croat

29b. Stems with only a few cataphylls, these usually semi-intact or with a few, thin, disorganized fibers.

32a. Blades drying reddish brown to dark yellow-brown; peduncles usually less than half as long as the spathe, straight below the spathe; spathe tube reddish purple to red outside; Costa Rica, Colombia, and Ecuador, 200–1300 m ..... *P. dodsonii* Croat & Grayum

32b. Blades drying dark gray-brown to olive-green, typically somewhat blackened above; peduncles usually as long as or longer than the spathe, frequently bent just below the spathe; spathe tube greenish on outside; Panama, 0–800 m ..... *P. panamense* K. Krause

1b. Blades with posterior rib (union of basal veins) not naked along the sinus, flanked with laminar tissue.

33a. Petioles conspicuously scaly distally; terrestrial (except *P. verrucosum*).

34a. Blades less than 25 cm long; petiolar scales close and overlapping, broad, usually less than 3 times longer than wide; endemic to El Copé region of Panama, ca. 800 m ..... *P. hammelii* Croat

34b. Blades usually more than 30 cm long; petiolar scales more widely scattered, many times longer than wide.

35a. Plants terrestrial; stems usually creeping laterally across the ground; spathes glabrous; Mexico and Guatemala, 580–1900 m ..... *P. glanduliferum* Matuda subsp. *glanduliferum*

35b. Plants appressed hemiepiphytic climbers; stems usually climbing trees; spathes conspicuously covered with slender scales, Costa Rica to Peru, 200–1500 m (mostly >500 m) ..... *P. verrucosum* L. Mathieu ex Schott

33b. Petioles glabrous and smooth distally, at least not conspicuously scaly; usually hemiepiphytic.

36a. Plants consistently terrestrial; petioles D-shaped with raised margins and a medial rib; spathe tube greenish to whitish within (or usually reddish on Pacific slope of Costa Rica); Nicaragua (Zelaya) to Panama, Colombia, and Ecuador; mostly 0–750 m ..... *P. grandipes* K. Krause

36b. Plants usually hemiepiphytic (*P. tysonii* frequently terrestrial in some habitats); petioles terete to subterete; spathe tube maroon to red or violet-purple within.

37a. Spathe not at all constricted above the tube, the spathe wall usually to ca. 1 cm thick midway; leaf blades very coriaceous, minor veins etched in the upper surface of fresh leaves; central Costa Rica to western Panama, 1100–2600 m ..... *P. crassispathum* Croat & Grayum

37b. Spathe visibly constricted above the tube (except only weakly constricted for *P. antonioanum*), the wall usually less than 3 mm thick except at very base; leaf blades not markedly coriaceous, minor veins never etched into surface of fresh leaves.

38a. Primary lateral veins frequently 10 or more per side; spathe tube white to pale green within (sometimes tinged red at very base); Nicaragua to S Ecuador and to Venezuela; 20–1400 m ..... *P. tenue* K. Koch & Augustin

38b. Primary lateral veins usually fewer than 10 per side (to 10 in *P. tysonii*); spathe tube red to red-violet, maroon, or violet-purple throughout within.

39a. Blades markedly sinuate along the margins; Mexico (Veracruz), less than 500 m ..... *P. subincisum* Schott

39b. Blades with the margins entire, not at all sinuate.

40a. Fresh cataphylls usually red; petioles and midribs lacking conspicuous purplish spots; basal veins 5–10 per side.

41a. Blades with primary lateral veins typically 6–10 per side, upper surface drying somewhat blackened and smooth; cataphylls unribbed to weakly 1-ribbed; spathe tube green or merely tinged reddish outside; ovaries with fewer than 7 sub-basal ovules contained in an ovule sac; western and central Panama, 600–1500 m ..... *P. tysonii* Croat

41b. Blades with primary lateral veins usually 5–6 per side, upper surface drying dark brown to gray-brown with prominulous cross-veining; cataphylls sharply 2-ribbed; spathe tube dark maroon outside; ovaries with about 30 axile ovules not contained in an envelope; endemic to Veraguas and Coclé Provinces at 850–1150 m ..... *P. antonioanum* Croat

40b. Fresh cataphylls green (purplish-spotted in *P. edenudatum* and *P. grayumii*); petioles and midrib frequently purplish-spotted; basal veins usually 3–5 per side.

42a. Blades mostly more than 1.8 times longer than wide; petioles 0.85–0.90 times as long as the blade; dried blades without secretory ducts visible on lower surface; Panama, 110–1150 m ..... *P. edenudatum* Croat

42b. Blades mostly less than 1.8 times longer than wide; petioles 1–1.4 times longer than the blade; dried blades with secretory ducts clearly visible on the lower surface; Costa Rica to central Panama, 0–1630 m ..... *P. grayumii* Croat

Key 4: Vines with Cordate Blades and Deciduous Cataphylls

[Note: None of the species in this group have the posterior rib of the leaf blades naked along the sinus except *P. brunneicaule*, *P. hederaceum*, *P. mexicanum*, and sometimes (weakly so) *P. coloradense*, *P. cotonense*, *P. sulcicaule*, *P. wilburii*, and *P. zhuanum*.]

1a. Internodes elongate, usually much longer than broad; plants usually vines or at least prominently scandent.

2a. Blades with the posterior rib (coalesced basal veins) not naked (i.e., not running on the margin of the sinus).

3a. Stems coarsely asperous, covered with branched scales or setose-pubescent.

4a. Blades ovate-triangular, subcoriaceous; posterior lobes slender, usually flaring; stems reddish brown, covered with trichome-like, frequently branched scales; berries pale yellow; styles very short; occurring usually in wet habitats; Nicaragua to Panama and South America, 60–280(1300) m ..... *P. brevispathum* Schott

4b. Blades ovate-cordate, thin; posterior lobes directed toward one another at maturity; stems greenish, covered with elongate setae; berries pale orange to red or reddish orange; usually occurring in dry habitats; Mexico to Panama, the West Indies, and South America, 0–1500(2500) m ..... *P. jacquinii* Schott

3b. Stems smooth, not covered with branched scales.

5a. Petioles prominently flattened dorsiventrally with the lateral margins sometimes acute; Nicaragua to Ecuador, 10–1500 m ..... *P. platypetiolatum* Madison

5b. Petioles terete to subterete, not prominently flattened dorsiventrally.

6a. Peduncles usually much shorter than the spathe, usually less than 7 cm long at anthesis, drying 6–10 mm diam.; ovules many (usually 10–20) per locule.

7a. Leaf blades narrowly ovate-elliptic or triangular-sagittate or triangular-hastate, usually 1.8 times or more longer than wide; posterior rib more than 3 cm long.

8a. Leaf blades narrowly ovate-elliptic; posterior lobes about as broad as long, directed toward the base; sinus ± V-shaped; ovules ca. 20 per locule; Mexico (Chiapas), 0–1000 m ..... *P. breedlovei* Croat

8b. Leaf blades triangular-sagittate to triangular-hastate; posterior lobes typically much longer than broad, directed somewhat outward; sinus usually not V-shaped but parabolic to spathulate; ovules usually 1–2 per locule; Mexico to Colombia, 0–1900 m ..... *P. mexicanum* Engl.

7b. Leaf blades ovate, usually only slightly longer than wide (rarely to 1.9 times longer than wide in *P. hederaceum*); posterior rib virtually lacking or to at most 1 cm long.

9a. Stems drying dark reddish brown, prominently ribbed, usually densely warty; Costa Rica to Ecuador and Suriname; (250)300–900 m ..... *P. hederaceum* var. *kirkbridei* Croat

9b. Stems drying either green and only weakly striate, or light yellowish brown and deeply fissured on drying.

10a. Stems drying yellowish brown, prominently ridged, smooth and glossy; spathe tube violet-purple outside; Costa Rica to Ecuador, 0–1600 m ..... *P. purpureoviride* Engl.

10b. Stems drying greenish, weakly striate, matte; spathe tube green outside; Mexico to West Indies, widespread in South America ..... *P. hederaceum* (Jacq.) Schott

6b. Peduncles frequently as long as or longer than the spathe, sometimes more than 7 cm long, usually drying 3–4 mm diam.; ovules 1 or 2 per locule.

11a. Leaf blades lacking any obvious primary lateral veins; stems prominently sulcate-ribbed even when fresh; ovules 1 per locule; SE Costa Rica to central Panama; 100–700 m ..... *P. sulcicaule* Croat

11b. Leaf blades with obvious primary lateral veins; stems smooth (or at least not regularly and prominently sulcate-ribbed longitudinally when fresh); ovules 2 per locule; Panama (Darién); 850–1560 m ..... *P. clewellii* Croat

CORDATE VINES WITH DECIDUOUS CATAPHYLLS AND BLADES WITH NAKED POSTERIOR RIBS

2b. Blades with the posterior rib naked and running on the margin of the sinus for usually 1.5 cm or more (sometimes to as little as 1 cm in *P. smithii*).

12a. Stems setose-pubescent; blades membranaceous on drying; spathe tube inflated, with considerable space between the inner surface of the spathe and the spadix; pistils elongated at apex into a style to ca. 5 mm long; Mexico to Panama, Cuba, and northern South America; 0–1500(2500) m ..... *P. jacquinii* Schott

12b. Stems glabrous; blades coriaceous to subcoriaceous on drying; spathe not inflated-bulbous at base, fitting tightly over spadix; pistils not at all elongated into a distinct stylar region.

13a. Stems prominently and regularly sulcate-ribbed when fresh.

14a. Blades less than 24 cm long, lacking obvious primary lateral veins; petioles to 21 cm long; NE Costa Rica to Isthmus of Panama; 100–700 m ..... *P. sulcicaule* Croat

14b. Blades more than 26 cm long, with 3–4 obvious pairs of primary lateral veins; petioles more than 29 cm long; S Mexico to Guatemala; 700–1525 m ..... *P. verapazense* Croat

13b. Stems smooth or irregularly fissured but not regularly sulcate-ribbed when fresh.

15a. Blades mostly broadly ovate, usually more than 25 cm wide; posterior lobes usually broadly rounded, about as wide as long; stems drying light reddish brown with flaking epidermis; Costa Rica to Ecuador, 100–1300 m ..... *P. brunneicaule* Croat & Grayum

15b. Blades mostly ovate-triangular or triangular-sagittate to triangular-hastate, mostly less than 25 cm wide (sometimes broader in *P. smithii*); Mexico to Panama; 0–2000 m.

16a. Blades sagittate to hastate at base; posterior lobes 2–3 times longer than broad; posterior rib directed straight toward the apex of the posterior lobe and 1.5–3.5 cm distant from the posterior margin of the blade; Mexico to Panama, 0–1900 m ..... *P. mexicanum* Engl.

16b. Blades cordate or sagittate (rarely hastate in some forms of *P. wilburii*); posterior lobes usually less than 2 times longer than wide (except sometimes more than 2 times longer in *P. wilburii*, and then blades drying reddish brown, not greenish as in *P. mexicanum*); posterior rib mostly curved along and near the margin of the sinus, rarely more than 1 cm from the posterior margin of the blade.

17a. Cataphylls 2-ribbed; blades usually more than 35 cm long; petiole often with a purple distal ring; peduncle usually longer than the spathe; Mexico to Nicaragua, 40–1630 m ..... *P. smithii* Engl.

17b. Cataphylls 1-ribbed (rarely 2-ribbed); blades usually less than 36 cm long; petioles lacking a purple distal ring; peduncle usually shorter than the spathe (except often longer in *P. wilburii* var. *longipedunculatum*); central Costa Rica to central Panama, 0–2000 m ..... *P. wilburii* Croat & Grayum

CORDATE NON-VINES WITH DECIDUOUS CATAPHYLLS AND NON-NAKED POSTERIOR RIBS

1b. Internodes of mature stems broader than long or sometimes somewhat longer than broad but not elongate with scandent stems (possibly somewhat scandent in *P. breedlovei* and *P. sousae*); plants mostly appressed-climbing hemiepiphytes.

18a. Petioles either densely covered with scales or D-shaped with undulate-winged margins.

19a. Petioles terete, less than 1 cm diam., densely covered with conspicuous, spreading scales; blades almost as broad as long, the major veins on the lower surface densely puberulent; Panama to Ecuador; 0–1300 m ..... *P. squamipetiolatum* Croat

19b. Petioles sharply D-shaped or sharply flattened with undulate-winged margins, more than 1.5 cm diam., glabrous; blades much longer than broad; veins of lower surface glabrous; Panama (Chiriquí); 1100–1300 m ..... *P. fortunense* Croat

18b. Petioles glabrous, terete to merely obtusely flattened.

20a. Posterior rib naked along the sinus.

21a. Peduncle usually less than 10 cm long.

22a. Blades less than 25 cm long, the adaxial surface drying dark brown to yellow-brown.

23a. Blades ovate-triangular, 1.8–3 times longer than wide; posterior lobes 1.4–1.8

times longer than wide; inflorescence solitary; Panama (Chiriquí), 1750–2100 m ..... *P. knappiae* Croat

23b. Blades ovate, 1.3–1.6 times longer than wide; posterior lobes about as wide as long; inflorescences 2–3 per axil; Panama (Chiriquí), 1600 m ..... *P. coloradense* Croat

22b. Blades more than 35 cm long, the adaxial surface usually drying green to brownish green to grayish green to dark olive-green (sometimes dark brown in *P. zhuanum* or blackish in *P. smithii*).

24a. Petioles on drying not markedly flattened, 8–15 mm diam., usually greenish to dark brown; less than 360 m along the Caribbean coast in Costa Rica ..... *P. aromaticum* Croat & Grayum

24b. Petioles on drying markedly flattened, to 3–6 cm diam., often yellowish; 700–900 m, Coclé Province, Panama ..... *P. zhuanum* Croat

21b. Peduncle usually 10 or more cm long.

25a. Leaf blades with margins convex in lower ½ of blade.

26a. Stem drying light brown; epidermis often flaking; petioles spongiose, but drying moderately smooth, flattening to ca. 1 cm wide; blades drying thin and lacking conspicuous secretory canals; 40–1630 m (mostly less than 600 m), Mexico to Nicaragua ..... *P. smithii* Engl.

26b. Stem drying dark brown; epidermis sulcate or cracked but not flaking; petioles firm, drying heavily wrinkled, flattening to 3–6 cm wide; blades drying coriaceous with conspicuous secretory canals; 700–900 m, Panama (Coclé) ..... *P. zhuanum* Croat

25b. Blades with margins straight to concave in lower ½ of blade; Costa Rica and Panama.

27a. Leaf blades drying pale yellow-green, lacking any sign of secretory ducts on lower surface; ovules 1 per locule; Costa Rica, 1350–1400 m ..... *P. straminicaule* Croat

27b. Leaf blades drying dark olive-green or dark brown, with secretory ducts visible alternating with the minor veins on lower surface; ovules 4–5 per locule; near Costa Rican–Panamanian border, 1100–1950 m ..... *P. cotonense* Croat

20b. Posterior rib not naked along the sinus, or weakly and obscurely naked near its base.

28a. Blades with posterior lobes turned inward and overlapping; peduncles slender, drying ca. 2–4 mm diam.; 850–1560 m, Serranía de Pirre, Darién Province, Panama ... *P. clewellii* Croat

28a. Blades with posterior lobes never overlapping (except sometimes in *P. ferrugineum*), usually directed backward or somewhat outward; peduncles stout, usually 5–10 mm diam. on drying.

29a. Spathe barely or not at all constricted near the middle or above the tube portion; sterile staminate portion of the spadix often conspicuously (50%) broader than the pistillate portion at anthesis; Mexico to Guatemala, 70–2500 m ..... *P. advena* Schott

29b. Spathe usually visibly constricted above the tube (usually somewhat below the middle); sterile staminate portion of the spadix narrower to only slightly broader than the pistillate portion at anthesis.

30a. Inflorescences 1–3 per axil; spathes less than 11 cm long (except 9.5–18 cm long in *P. brenesii*).

31a. Primary lateral veins mostly more than 8 pairs; minor veins etched-sunken on upper blade surface; lower blade surface ± bluish green; 800–2200 m, Costa Rica and Panama ..... *P. brenesii* Standl.

31b. Primary lateral veins 4–8 pairs (sometimes to 9 pairs in *P. sagittifolium*); minor veins flat or raised on upper blade surface; lower blade surface medium green to yellow-green, not bluish green; Mexico and Belize.

32a. Leaf blades ca. 1.6 times longer than wide; ovules 1–7 per locule.

33a. Blades drying gray-green below; sap white; ovules 1 per locule; Belize, less than 500 m ..... *P. dwyeri* Croat

33b. Blades drying dark yellow-brown below; sap clear, turning brown?; ovules 4–7 per locule; Panama, 1600 m ..... *P. coloradense* Croat

32b. Leaf blades ca. 1.8–2 times longer than wide; ovules 2–4(5–8) or ca. 20 per locule; Mexico (Chiapas, 1300 m) or widespread, Mexico to South America, 150–2700 m.

34a. Blades ca. 1.8 times longer than wide; inflorescence 1 per axil; ovules 20 per locule; Mexico (Chiapas), 1300 m ..... *P. breedlovei* Croat

34b. Blades 1.85–2 times longer than wide, inflorescences 1–3 per axil; Mexico (Veracruz) to Colombia, 0–1800 m ..... *P. sagittifolium* Liebm.

30b. Inflorescences 4–6 per axil; spathes 15–23 cm long.

35a. Cataphylls usually more than 25 cm long; blades usually more than 55 cm long, drying coriaceous, reddish brown, with minute interrupted ridges on lower surface; Panama, 100–770 m ..... *P. ferrugineum* Croat

35b. Cataphylls less than 25 cm long; blades usually less than 55 cm long, drying subcoriaceous, brown to olive-green, smooth or minutely ridged but not with interrupted ridges on lower surface; Mexico (Chiapas), 490–1400 m ..... *P. sousae* Croat

Philodendron advena Schott, Oesterr. Bot. Wochenbl. 5: 289. 1855. TYPE: Mexico. Exact location uncertain, described from living material, *Schott s.n.* (lectotype, here designated, L 900230 (89889152)). Figures 37–40, 73.

Philodendron subovatum Schott, Osterr. Bot. Wochenbl. 5: 289. 1855. TYPE: Western Mexico: a cultivated collection prepared by Schott (holotype, W now destroyed). Field Museum Photo 29864 (neotype, here designated; duplicate photo at MO).

Philodendron monticola Matuda, Madroño 10: 170. 1950. TYPE: Mexico. Chiapas: Sierra Madre, Pacific slope, Colonia San Juan Panamá, 50 km E of Escuintla, 1600 m, *Matuda 18169* (holotype, MEXU; isotypes, DS, NY, UCLA).

Philodendron jamapanum G. S. Bunting, Gentes Herb. 9: 336, fig. 242. 1965. TYPE: Mexico. Veracruz: Coscomatepec–Huatusco, Route 155 at Rió Jamapa, *Moore & Bunting 8872* (holotype, BH).

Terrestrial, epilithic, or hemiepiphytic; stem appressed-climbing, to 2 m long, sap brownish orange; internodes weakly glossy, 2–4 cm long, 1.5–2.5(5.5) cm diam., longer than broad, sometimes obtusely flattened on one side, medium green to gray-green, drying brown to yellow-brown, epidermis smooth to closely fissured; roots few per node, drying dark brown to yellow-brown, epidermis sometimes flaking; cataphylls subcoriaceous, 7.7–45 cm long, sharply D-shaped to sharply 2-ribbed, rarely weakly 2-ribbed, light green to whitish, tinged reddish, generally deciduous intact, weakly emarginate at apex, margins clear. LEAVES erect-spreading to spreading with blades pendent; **petioles** 30–45(65) cm long, 7–18 mm diam., erect-spreading, subterete to D-shaped, somewhat spongy to moderately firm, obtusely flattened adaxially, sheath 3–11 cm long; **blades** ovate-cordate to sagittate, subcoriaceous, moderately bicolorous, gradually acuminate at apex, cordate at base, (32)41–47(64) cm long, 16.5–40 cm wide (1.2–2.5 times longer than wide; 1–1.5 times longer than petioles), margins hyaline, upper surface dark green, drying dark brown to blackened, sometimes yellow-green, lower surface slightly more glossy, paler, drying yellow-brown to reddish brown, sometimes greenish brown; anterior lobe 20.5–53 cm long, 12–40 cm wide (3.4–3.8 times longer than posterior lobes); posterior lobes rounded, 6–14(20) cm long, 5.4–15(20) cm wide, directed toward base; sinus ± parabolic to V-shaped or spathulate, 8–15 cm deep; midrib broadly convex to flat, slightly paler than surface above, convex and slightly paler below; basal veins 3–6 per side, with 0–1(2) free to base, coalesced (0.4)1.3–4(8.5) cm; posterior rib not naked or obscurely naked to 1 cm at base; primary lateral veins (3)4–6 per side, departing midrib at a (45)50–60(80)° angle, straight or weakly arcuate to the margins, flat to sunken and paler than surface above, convex below; minor veins weakly raised, moderately visible, arising from both the midrib and primary lateral veins. INFLORESCENCES spreading-pendent, 1–2(4) per axil; peduncle 5–13.5(17) cm long, 7–11 mm diam.; **spathe** coriaceous, (6.5)12–19 cm long ((0.7)1.4–2.4 times longer than peduncle), weakly or not at all constricted above the tube, acuminate, usually greenish throughout, broadest at or below the middle; spathe blade greenish white outside, spathe red to maroon or greenish white, glossy inside; spathe tube sometimes reddish outside, 5–8 cm long, 2.5–3.5(5) cm diam., red to maroon or dark violet-purple, pale-lineate, glossy inside; **spadix** stipitate to 4 mm long; clavate to cylindrical, bluntly pointed at apex, 11.5–14 cm long, broadest at the middle or ± uniform throughout; pistillate portion 3.3–6.9 cm long, 1.2–2.7 mm diam. at middle, narrowed somewhat at both ends; staminate portion 5–9.2 cm long; fertile staminate portion tapered to cylindrical or clavate, usually longer than pistillate portion, 11–14 mm diam. at base, 8–15 mm diam. at middle, 5–7 mm diam. ca. 1 cm from apex, broadest below middle, equal in length to pistillate portion, narrower than pistillate and sterile portions; sterile staminate portion, 11–30 mm diam., usually broader than pistillate portion at anthesis; pistils 1.7–8.5 mm long, 1.3–2.9 mm diam., ovary (5)6–8-locular, with basal to sub-basal placentation; ovules 1–4 per locule, arranged digitately in translucent ovule sac, 0.2–0.6(1.5) mm long, equal in length to funicle; funicle adnate to lower part of partition, style 0.9–3 mm long, similar to style type B; style apex flat; stigma discoid to subdiscoid; thecae cylindrical to elliptical, 0.5 mm wide, contiguous. INFRUCTESCENCE with spathe green outside, dark purple-violet inside, 11.5–14 cm long; berries white to yellowish; seeds 1(3–4) per locule, oblong-ellipsoid, sometimes obovoid, 1.7–2.2 mm

long, 0.7–1.8 mm diam., with clear longitudinal and faint latitudinal striations and speckled with shiny, silver raphide cells; funicular scar knob-like, clear, thicker than the seed body.

Flowering specimens of *Philodendron advena* have been collected in post-anthesis condition virtually throughout the entire year. Mature fruits have been collected less consistently with July and August the only consecutive months without fruits reported.

Philodendron advena ranges from Central Mexico (Veracruz) along the Atlantic slope to Chiapas and then along both the Pacific and Atlantic slopes to southern Guatemala (Santa Rosa and Chiquimula Departments). It occurs at 70 to 2500 (mostly above 1000) m elevation in a wide variety of vegetation types, including "Selva Alta Perennifolia," "Bosque Caducifolia," "Selva Mediana Subperennifolia," and "Bosque Caducifolia."

Philodendron advena is a member of *Philodendron* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. The species is distinguished by internodes longer than broad, its two-ribbed, generally deciduous cataphylls, terete to obtusely flattened, somewhat spongy petioles (about as long as the blades), and by its generally coriaceous, ovate-cordate, usually dark brown to blackened-dried to somewhat sagittate-lobed blades with rounded lobes with usually four to six primary lateral veins, and usually one to two green inflorescences with the inner surface reddish to purplish.

Material from the Pacific slope in Chiapas State, Mexico, and in adjacent Guatemala often dries somewhat more greenish. This was described by Matuda as *P. monticola* Matuda. Considering the variability in the species, that taxon is not warranted. Though not closely related to *P. purulhense* Croat, *P. advena* is perhaps most easily confused with that species, because both may have similar ovate, black-drying leaves. *Philodendron purulhense* differs from *P. advena* in its persistent cataphylls, a more or less elliptic spathe scarcely constricted above the tube, and ovaries with axile placentation and 13–20 ovules per locule.

Philodendron advena is probably most closely related to the equally ecologically versatile *P. sagittifolium*, which occurs throughout much of its range. *Philodendron sagittifolium* is distinguished by having usually longer, more prominently sagittate blades (averaging 1.5–3 times longer than broad), which dry typically reddish brown rather than blackened. In contrast, *P. advena* has blades averaging 1.5 times longer than broad (ranging from 1.3 to 1.8 times longer). Both *P. advena* and *P. sagittifolium* have five to eight locules per pistil with up to three more or less basal ovules (or they have the funicle adnate to the lower part of the axillary wall but extending down to the base).

Two Oaxaca collections are noteworthy. *Moore & Bunting 8891* from above Valle Nacional in the Serranía de Juarez of Oaxaca dried greenish brown on the lower surface and gray-brown above. Also unusual is *Moore & Bunting 8919* (collected near *8891*), which dried reddish brown. This collection was discussed as possibly distinct by Bunting (1965). Aside from the color of the blades upon drying, there is nothing else out of the ordinary with the collection (see fig. 235 in Bunting, 1965).

Additional specimens examined. GUATEMALA. **Alta Verapaz**: near Chirriacté, on the Petén Highway, ca. 900 m, *Standley 92192* (F); ca. 6 km NE of Panzós, 800 m, *Croat 41689* (MO); 7 mi. up the road to Oxec, 700 m, *41651* (MO); Finca Argentina, 15 mi. W of Telemán, 550–650 m, *41571* (MO); 2–4 mi. E of Tamahú, 9–11 mi. E of Hwy. CA-14 to Cobán, 700–800 m, *41498* (MO); near Tactic, ca. 1500 m, *Standley 70495* (F); near Tactic, above Río Frío, 1400–1500 m, *90484* (F). **Chiquimula**: Cerro Tixixí, 3–5 mi. N of Jocotán, 500–1500 m, *Steyermark 31563* (F). **Quezaltenango**: in reserve INDE "Santa María," km 99, 14°45′N, 91°32′W, *Croat & Hannon 63430* (K, MO, US, USCG); El Pocito, S of San Martín Chile Verde, on road to Colomba, ca. 2200 m, *Standley 85039* (F), *85093* (F); between San Martín Chile Verde and Colomba, above Mujuliá, ca. 1800 m, *85723* (F), *85561* (F); between Finca Pirineos and Finca Patzulín, 1200–1400 m, *86875* (F); Río Samalá, near Santa María de Jesús, 1500–1650 m, *84571* (F), *84669* (F). **San Marcos**: Canjulá–La Unión Juárez, near SE portion of Volcán Tacaná, 2000–3000 m, *Steyermark 36407* (F); Volcán Tajumulco, 1400–1700 m, *37391* (F); ca. 3.3 mi. above Finca Armenia, above San Rafael, 1600 m, *Croat 40963* (MO, NY); San Rafael–Pie de la Cuesta–Palo Gordo, near Aldea Fraternidad, 1800–2400 m, *Williams et al. 26014* (F, NY). **Santa Rosa**: Cenaguilla, 4000 ft., *Heyde & Lux 4281* (G, NY, US). **Zacapa**: summit of Sierra de las Minas, vic. of Finca Alejandria, 2500 m, *Steyermark 29855* (F); Río Lima, Sierra de las Minas, below Finca Alejandria, 2000 m, *30026* (F). MEXICO. **Chiapas**: Lagos de Montebello, 3 mi. W of Dos Lagunas, 1460 m, *Croat 46636* (MEXU, MO), *46655* (MO); ca. 6 mi. NW of Pueblo Nuevo Solistahuacán, vic. km 99, 1900–1950 m, 17°07′N, 92°52′W, *Croat & Hannon 65193* (MEXU, MO); 8 mi. NW of Pueblo Nuevo Solistahuacán, 1900–1950 m, *Croat 46429* (MEXU, MO), *46430* (MEXU, MO); Ixtapa–Pichucalco, *47777* (B, K, MO); Bochil–Pichucalco, 3.4 km W of El Anepo, 1860 m, *Croat 78610* (CHIP, CM, K, MO, NY); San Cristóbal–Palenque, 97 km NE of San Cristóbal, 1130 m, 17°27′N, 92°04′W, *Hammel et al. 15624* (MO); Palenque–Bonampak, 89–90 mi. SW of Palenque, 350–370 m, *Croat 40221* (MO); San Juan Panamá, Escuintla, 1800 m, *Matuda 18488* (MEXU, NY); Cascada, Siltepec, 1800 m, *19643* (MEXU); Paso Pashital, Sierra Madre de Chiapas, 1800 m, *37585* (MEXU); Cerro Brujo, Ocozozoautla de Espinosa, *MacDougall 415* (MEXU); ca. 6 mi. SW of Motozintla de Mendoza, ca. 1850 m, *Croat 47246* (MO); 26–30 mi. N of Motozintla de Mendoza, 9.5–4.5 mi. S of Siltepec, 1000–1300 m, *47462* (MO); Ojo de Agua, Soconusco, *Nakamura 38* (DS); San Fernando–Moravillas,

4–66 mi. NW of San Fernando, 840–940 m, 16°53′N, 93°16′W, *Croat & Hannon 65006* (B, MEXU, MO, US); Mpio. Angel Albino Corzo, above Finca Cuxtepec, 1380 m, *Breedlove 52073* (DS); Mpio. Berriozábal, 13 km N of Berriozábal, 900 m, *35438* (DS); 16 km NW of Rizo de Oro, 1600 m, *Breedlove & Smith 31382* (DS); Mpio. Ocosingo, Laguna Ocotal Grande, 3300 ft., *Breedlove 15683* (F, MICH); Mpio. Rayón, Selva Negra, 10 km above Rayón Mezcalapa, along road to Jitotol, 1700 m, *23291* (DS); Mpio. Union Juárez, Volcán Tacaná, above Talquian, 2200 m, *Breedlove & Almeda 47712* (CAS); Mpio. Villa Corzo, E base of Cerro Tres Picos, near Cerro Bola, 1500 m, 16°10′N, 93°15′W, *Breedlove & Thorne 30193* (DS). **Oaxaca**: Sierra de Juárez, Highway 175, 6–14 mi. from bridge at Valle Nacional, ca. 580 m, *Moore & Bunting 8891* (BH); Vista Hermosa, 17.9 mi. from bridge at Valle Nacional on road to Oaxaca, *8919* (BH); 660 m, *Croat 78721* (CHIP, MO); 4.3–6 mi. above bridge at Valle Nacional, 705 m, 17°44′N, 96°19′W, *Croat & Hannon 65549* (CM, MEXU, MO, NY, US); 14 mi. W of Valle Nacional, 1210 m, *Croat 39783* (MEXU, MO), *39796* (MO); 21.5 mi. above Valle Nacional, 1660–1670 m, *48108* (MO); Teotitlán del Camino–Chilchotla, 2.2 mi. beyond turnoff to Huautla de Jiménez, 2270 m, *48335* (CM, MO); 3.8 mi. past turnoff to Huautla de Jiménez, 2265 m, *48369* (MO); Ixtlán, Río Soyolapan watershed, 765–805 m, 17°37′N, 96°17′W, *Boyle et al. 3943* (MO). **Tabasco**: Teapa–Tacotalpa, 3.1 mi. E of Teapa, ca. 0.25 mi. S of highway, 150 m, 17°33′N, 92°59′W, *Croat & Hannon 65376* (MO); Mpio. Teapa, 7 km SE of Teapa on road to Tacotalpa, Rancho San Enas, Sierra Madrugal, 70 m, 17°35′N, 92°50′W, *Hammel & Morello 15519* (MO, NY); Río Puyacatengo, Sierra Madrigal, 7 km E of Teapa, trail from Centro Regional del Sureste of Universidad Autonoma Chapingo, 300 m, 18°32′N, 92°55′W, *Schatz et al. 1178* (MO). **Veracruz**: Veracruz–Oaxaca, Uxpanapa, 150 m, 17°05′N, 84°35′W, *Hammel & Merello 15563* (MO); above San Jose de Gracia, 1 mi. S of hwy. between Córdoba and Veracruz, 750 m, *Croat 39618* (MO); Conejo–Huatusco, at km 45, barranca de Santa María, across hwy. from Hacienda El Mirador, *Moore & Bunting 8856* (BH); ca. 1200 m, *Croat 44013* (MO); Mendoza–Orizaba, Sierra San Cristóbal, Highway 150-D, ca. 3 km SW of Orizaba, 1260–1400 m, *Croat 39549* (CM, MEXU, MO); Fortín-Huatusco, Highway 125, 300 m, 19°06′N, 97°02′W, *Croat & Hannon 63107* (B, COL, CR, CM, F, G, INPA, K, LL, M, MO, NY, QCA, P, PMA, US, VEN); Acajete, 1750 m, *Cházaro & Robles 3115* (WIS); Mpio. Coacoatzintla, 1300 m, *Cházaro 1053* (F); Mpio. Ixhuacan, Río Ixhuacan, El Aguacate–Putlanalan, Puebla, 1500 m, *Cházaro & Cházaro 4068* (MO, WIS); Mpio. Jalapa, 8 km NW of Consolapan, 1525 m, ca. 19°30′N, 96°59′W, *Nee 29683* (MO, NY); Coapexpan, 1470 m, *Young 35* (F, MO); Mpio. Tlanelhuayocan, Barranca del Pixquiac, Rancho Viejo–Ya Vega, 1650 m, *Cházaro & Ramarillo 3895* (MO, WIS); Mpio. Yecuatla, Los Capulines, near Paz de Enríquez, ca. 8 km N of Chiconquiaco, 1400–1600 m, 19°47′N, 96°49′W, *Taylor et al. 147* (F, MO, NY).

Philodendron albisuccus Croat, sp. nov. TYPE: Panama. Darién: Parque Nacional del Darién, middle slopes on W side of Cerro Pirre, 800–1500 m, 7°56′N, 77°45′W, 29 June 1988, *Croat 68940* (holotype, MO–3589989; isotypes, B, COL, K, PMA, US). Figures 41–43.

Planta hemiepiphytica; internodia 2–3 cm longa, 2.8 cm diam.; succus albus, in sicco calcareus; cataphylla leviter 1-costata vel acute 2-costata, persistentia ut fibrae tenues, pallidae; petiolus usque 51–72 cm longus, subteres, leviter complanatus basi usque ad medium; lamina anguste ovata, cordata basi, 50–66 cm longa, 24.5–42 cm lata; inflorescentia 1; pedunculus (3.7)7–12 cm longus; spatha 13.5–14.5 cm longa, extus viridis, intus pallide flaviviridis; pistilla 5–6-locularia; locules cum 18–20 seminibus; baccae albae.

Hemiepiphytic; stem ± appressed-climbing, to 75 cm long, to 2.8 cm diam., sap chalky white; internodes short, usually sparsely covered with cataphyll fibers, 2–3 cm long, 2.8 cm diam., dark green; roots brownish, few per node, epidermis smooth to flaking and peeling; cataphylls thin, to 40 cm long, weakly 1-ribbed to sharply 2-ribbed, sparsely short-lineate, persisting as thin, pale fibers at upper nodes, then deciduous; **petioles** 51–72 cm long, 3–7 mm diam., erect-spreading, subterete, dark green, weakly flattened from near base to middle, obtusely sulcate at the base adaxially, surface semiglossy; **blades** narrow ovate, subcoriaceous, splitting, long-acuminate at apex (the acumen inrolled), cordate at base, 50–66 cm long, 24.5–42 cm wide (1.6–2 times longer than wide), (ca. about equal in length to petiole), broadest just below point of petiole attachment, upper surface dark green, semiglossy, lower surface semiglossy, moderately paler, drying yellow-green; anterior lobe 37–48(54.5) cm long, 23.1–27.4(42.4) cm wide (4.2–4.4 times longer than posterior lobes); posterior lobes 8.5–11.5(16.5) cm long, 9.7–12(18.5) cm wide; sinus hippocrepiform; midrib flat, concolorous above, bluntly acute, slightly paler than surface below; basal veins 3–5 per side, with 1 free to base, third and higher order veins coalesced 0.5–2 cm long, the fifth and sixth veins sometimes coalesced to 5 cm long; posterior rib naked, raised; primary lateral veins (4)6–7(8) per side, departing midrib at a 60–65° angle, sunken above, raised to convex below; interprimary veins darker than surface; minor veins arising from both the midrib and primary lateral veins; lesser veins obscure to visible. INFLORESCENCES 1 per axil; peduncle (3.7)7–12 cm long, 3–3.5 mm diam., pale green; **spathe** semiglossy, 13.5–14.5 cm long (1.2–1.8 times longer than peduncle), weakly constricted above the tube, green throughout, pale yellow-green (greenish brown post-anthesis) within; spathe tube densely short pale lineate outside, 5–7 cm long; **spadix** 12 cm long at anthesis; pistillate portion 4.3 cm long in front, 3 cm long in back, 8 mm diam. midway, 7 mm diam. at apex; staminate portion to 10 cm long; fertile staminate portion to 9 mm diam. toward apex, somewhat narrower just

above the sterile portion, to 5 mm diam. 1 cm from apex; sterile staminate portion 9 mm diam.; pistils 6–6.3 mm long, 1.8–2.5 mm diam., ovary 5–6-locular, with axile placentation; ovules 2-seriate, style similar to style type B; style apex flat; stigma subdiscoid. INFRUCTESCENCE 6.4 cm long, 3 cm diam.; berries white; seeds 18–20 per locule.

Flowering in *Philodendron albisuccus* is poorly known with a flowering collection seen in October, immature fruits in June, and nearly mature fruits in July.

Philodendron albisuccus is endemic to Panama, known only from the Serranía de Pirre in Darién Province, at 800 to 1400 m elevation in *Premontane rain forest.*

Philodendron albisuccus is a member of *Philodendron* sect. *Philodendron* subsect. *Cardiobelium* ser. *Albisuccosa.* The species is characterized by its short internodes; thin, obscurely one-ribbed cataphylls, which persist at the upper nodes as thin, pale fibers; subterete petioles (about as long as the blades); the narrowly ovate, moderately cordate blades with a hippocrepiform sinus; and especially by the sap in all the cut plant parts, which promptly turns white and chalky upon exposure to air. Only one other species in Panama, *P. cretosum* Croat & Grayum, has chalky sap. Though both species have chalky sap (a rare feature for *Philodendron*) and 18–20 ovules per locule, I do not believe them to be closely related as they show no other features in common. *Philodendron cretosum* differs most particularly in having slender oblong-lanceolate blades that are 5.1–8.3 times longer than wide (vs. 1.6–2 times longer than wide for *P. albisuccus*). *Philodendron albisuccus* also has the much longer petioles (51–72 cm long vs. 10–23 cm long for *P. cretosum*), more broadly spreading primary lateral veins (60–65° vs. 25–45° angle for *P. cretosum*). In addition, *P. albisuccus* has minor veins more distinct than those of *P. cretosum.*

The species is superficially similar to *P. alticola* Croat and *P. straminicaule* Croat & Grayum, both of which have blades of similar size, shape, and color upon drying. Both differ by having the inner surface of the spathe red rather than green.

Additional specimens examined. PANAMA. **Darién**: Cerro Sapo, ca. 5 km S of Garachiné, 600–800 m, 7°59′N, 78°25′W. *Hammel et al. 14820* (MO, US); Cerro Pirre region, Altos de Nique–Cerro Pirre, ca. 8 km N of Alturas de Nique, ca. 8 km W of Cana Gold Mine, 1430–1480 m, *Croat 37851* (MO, PMA); Río Cana–Río Escucha Ruido, along ascent of Serranía de Pirre above Cana Gold Mine, 1310–1430 m, *37830* (MO, US); Río Cana, SW of Cerro Pirre, vic. of old gold mine at Cana, 1400 m, *27319* (MO); Parque Nacional Darién, slopes of Cerro Mali, headwaters of S branch of Río Pucuro, ca. 22 km E of Pucuro, 1300–1400 m, 8°04′30″N, 77°14′W, *Cuadros et al. 3961* (MO).

Philodendron alticola Croat & Grayum, sp. nov. TYPE: Panama. Chiriquí: Parque La Amistad, 3.5 mi. W of Cerro Punta, 2 km inside park along old abandoned roads and trails, 800 m, 8°53′N, 82°35′W, 28 Mar. 1993, *Croat 74906* (holotype, MO–4343624–5; isotypes, B, CR, F, K, PMA, US). Figures 45–48.

Planta epiphytica aut hemiepiphytica; internodia (1.5–2)4–10 cm longa, 2–4 cm diam., in sicco pallide flavibrunnea, subtiliter costata; cataphylla usque 28 cm longa, incostata, in sicco pallide brunnea, decidua; petiolus 42–70 cm longus, 7–10 mm diam.; lamina ovato-sagittata, 44–72 cm longa, 21–44 cm lata, sagittata basi, in sicco brunnea supra, flavibrunnea infra; inflorescentia 1–2; pedunculus 5–12 cm longus; spatha 11.5–14(18) cm longa, viridis; pistilla (4)5–6(7)-locularia; loculi 12–18-ovulati.

Epiphytic or hemiepiphytic; stem appressed-climbing; internodes dark green, promptly gray-green, finally light brown, semiglossy, finely ribbed, (1.5–2)4–10 cm long, 2–4 cm diam., drying pale yellow-brown, epidermis sometimes loosening and flaking free in small patches; cataphylls sharply D-shaped with weakly raised margins, pale green, weakly glossy, drying thin, to 28 cm long, unribbed, drying pale brown, deciduous at lower nodes, persisting semi-intact at upper nodes with a few exposed pale fibers, in part persisting as pale fibers at lower nodes with a few pale fibers and small, thin fragments of pale brown epidermis. LEAVES erect-spreading to spreading; **petioles** 42–70 cm long, 7–10 mm diam., subterete, medium green, weakly glossy, faintly lineate, obtusely flattened adaxially, weakly spongy, drying greenish to blackened, slightly flattened toward the apex adaxially, surface drying ± matte, sometimes with portions of epidermis loose and bubbled, tan and translucent; sheathing subtending an inflorescence, to 6 cm long; **blades** narrowly ovate-sagittate, subcoriaceous to moderately coriaceous, semiglossy, somewhat bicolorous, weakly and shortly acuminate at apex, sagittate at base, 44–72 cm long, 21–44 cm wide (1.6–2 times longer than wide), (about as long as petioles), broadest somewhat above point of petiole attachment, upper surface dark green, matte, drying brown to greenish brown and almost matte, lower surface moderately paler and weakly glossy, drying yellow-brown; anterior lobe 34–35.5 cm long, margins convex; posterior lobes 13–26 cm long, 11–17 cm wide, directed downward; sinus obovate, 10–19 cm deep; midrib speckled, slightly paler, drying broadly convex, concolorous above, narrowly rounded, slightly paler, drying prominently convex, often flat and irregularly ridged, yellow-

ish brown below; basal veins 5–6 per side, with the first free to base, the second coalesced 1–5 cm, third and higher order veins coalesced 4–7.5 cm long; posterior rib naked for 1–3 cm; primary lateral veins 5–8 per side, those near end of blade departing midrib at a 50–65° angle, those in the lower one-half of blade departing at 80–95° angle, broadly curved to the margins, obtusely sunken and slightly paler, drying weakly raised above, convex and paler than surface, splayed out and downturned at the midrib, drying weakly raised below; interprimary veins inconspicuous; minor veins moderately distinct, fine, arising from both the midrib and primary lateral veins, drying prominulous, alternating with secretory canals appearing as intermittent lines, sometimes branched, blackened and minutely sunken. INFLORESCENCES erect, 1–2 per axil; peduncle ± terete, coarsely striate (coarser on spathe and base of tube, pale short-lineate otherwise), weaker toward apex, 5–12 cm long, drying 7–10 mm diam., pale green, drying dark brown; **spathe** coriaceous, 11.5–14(18) cm long, scarcely or not at all constricted midway, green to yellowish green throughout, acuminate; spathe blade dark green throughout, drying dark brown and unmarked, smooth outside, pale greenish white to white on upper two-thirds of blade inside; spathe tube 2.8–4 cm long, 2–3 cm diam., red to red-violet to purplish on lower one-third of tube inside; **spadix** 9–14 cm long; pistillate portion pale green, 0.8–1.2 cm long, 1–1.5 cm diam. throughout; staminate portion 8–12.5 cm long; fertile staminate portion creamy white, stubby, evenly and bluntly tapered to apex, 1.5–2 cm diam. throughout, broadest at the base, much broader than the pistillate portion; sterile staminate portion 1.5 cm diam.; pistils 3–4 mm long, 1.7–1.8 mm diam., ovary (4)5–6(7)-locular, with axile placentation; ovules 12–18 per locule, 2-seriate, weakly translucent, 0.4–0.5 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style similar to style type B; central style dome sometimes weakly developed; dried style base raised but flattened apically with a narrow, pale ring around its outer margin; stylar canals emerging as tiny funnels at base of small apical depressions and arranged separately in a ring, drying as minute funnels extending above the surface of the style boss; style apex weakly concave; central domes and small depressions surrounding stylar canal exits; stigma covering entire style apex; androecium truncate, oblong prismatic, margins irregularly 4–5-sided or 4–6-sided, 0.9–1 mm long; thecae ± oblong, ca. 0.3 mm wide; sterile staminate flowers in part prismatic, in part weakly clavate or irregularly 4–6-sided, 1.2–1.8 mm wide. INFRUCTESCENCE in early fruit to 14 cm long; spathe becoming dark brown with paler lines in tube; berries white with dried style bases ca. 2 mm long, brown, with a narrow smooth ring around its margin; seeds tan, ovoid, weakly mammiliform, 1.4–1.8 mm long, 1–1.2 mm diam.

Flowering in *Philodendron alticola* is documented by just a few collections and might be bimodal. Specimens in Panama were collected both in bud and immature fruit in February (nearly mid-dry season in Panama), but post-anthesis collections were also made in August and September. No mature fruits were seen. The region where *P. alticola* occurs is decidedly less seasonal (at least in terms of totally rainless days) than is much of the rest of Panama. This might induce a less seasonal flowering in *Philodendron.*

Philodendron alticola is known only from eastern Costa Rica and western Panama in the region adjacent to the frontier at 800 to 2500 m elevation in *Tropical Lower Montane wet forest* or possibly *Tropical Lower Montane rain forest.* It is one of the most high-ranging species of *Philodendron* subg. *Philodendron* Schott in Central America, hence the name "alticola" (meaning high-dweller).

Philodendron alticola is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* In addition to the high elevations at which it occurs, the species is characterized by having the internodes longer than broad and drying yellowish brown and finely ribbed; by its subterete petioles about twice as long as the blades, drying darkened and sometimes with bubbly epidermis; the ovate-sagittate blades, which dry mostly dark brown above and yellowish green below with conspicuous blackened, interrupted and sometimes branched secretory ducts; and by the usually paired, short-pedunculate inflorescences with the spathe scarcely constricted above the tube, green outside, white inside on the blade and red to purple on the tube within. The species is most similar to *P. straminicaule,* which is also subscandent and has similarly colored blades. That species differs in lacking prominent intermittent laticifers and the fertile staminate portion of the spadix constricted above the sterile portion; the sterile staminate portion of the spadix only slightly thicker than the pistillate portion; and a doughnut-shaped style with the style tubes in the bottom of a concavity upon drying. In addition, it has only 1 ovule per locule (vs. 12–18 per locule for *P. alticola*). In contrast, *P. alticola* has conspicuous laticifers, the staminate spadix scarcely or not at all constricted above the sterile

portion, and the sterile portion of the spadix much thicker than the sterile staminate portion. The dried style base of *P. alticola* is flat at the apex with erect, tubular-extensioned stylar pores.

The species is also similar to *P. schottianum* H. Wendl. ex Schott, which also shares the conspicuous latex canals on the lower blade surface and a similarly stubby spadix, but that species differs in having shorter internodes, cataphylls that persist as a dense mass of fibers (vs. semi-intact or as only a few pale fibers interspersed with small fragments of epidermis in *P. alticola*), by its petioles, which dry smoother and more matte, and by its more broadly ovate blades, which often have conspicuous cross-veins.

Additional specimens examined. COSTA RICA. **Limón**: Cordillera de Talamanca, Atlantic slope, Valle de Silencio, along Río Terbi, 0.5–1.5 airline km W of Costa Rican–Panamanian border, 2300–2400 m, 9°8′N, 82°57′W, *Davidse et al. 28735* (CR, MO); S side of unnamed cordillera between Río Terbi and Río Siní, 2–4 airline km W of Costa Rican–Panamanian border, 2300–2500 m, 9°9–11′N, 82°57–58′W, *Davidse et al. 28931* (MO). PANAMA. **Chiriquí**: vic. of Las Nubes, 2.7 mi. NW of Río Chiriquí Viejo, W of Cerro Punta, 2200 m, *Liesner 323* (MO, US), *325* (MO, US); Cerro Punta, Las Nubes, 2000 m, *Croat 26492* (MO).

Philodendron angustilobum Croat & Grayum, sp. nov. TYPE: Costa Rica. Heredia: Estación Biológica La Selva, confluence of Río Sarapiquí and Río Puerto Viejo, 10°26′N, 84°01′W, 50–80 m, *Grayum & Chavarría 8302* (holotype, MO). Figures 49–52, 74.

Planta hemiepiphytica; internodia 3–6(15) cm longa, 1.5–3 cm diam.; cataphylla 12–33 cm longa, acute 2-costata; petiolus subteres, 17–54 cm longus, 5–10 mm diam.; lamina profunde 3-lobata, 30–48 cm longa, 20–48 cm lata; in sicco atricana vel atribrunnea supra, flavibrunnea vel atricanibrunnea infra; lobis lateralibus manifeste patentibus, in sicco denigratis infra; inflorescentia 1–3; pedunculus (4.5)9–11(15) cm longus; spatha (11)13–18 cm longa, lamina spathae extus interdum suffusa alba; tubo spathae pallide viridi, extus interdum suffusa marronino basi; pistilla 7–10-locularia; loculi (1)2-ovulati.

Hemiepiphytic; stem appressed-climbing, growing to 2.5–6 m high in trees; internodes matte to weakly glossy, 3–6(15) cm long, 1.5–3 cm diam., dark green, drying gray (within 4–6 internodes), epidermis drying light brown, semiglossy, often peeling (underlying stem blackened), fissured transversely, longitudinally ridged; cataphylls soft (especially near base), 12–33 cm long, bluntly to sharply 2-ribbed or sharply 1-ribbed to near the apex then 2-ribbed below, green, sometimes tinged red, deciduous, persisting deciduous, intact; **petioles** 17–54 cm long, 5–10 mm diam., subterete, somewhat spongy, dark green, weakly flattened toward apex with an obscure medial rib adaxially, with adaxial margins rounded to weakly angular, surface weakly glossy, drying blackened; sheathing 3–9 cm long; **blades** deeply 3-lobed, subcoriaceous, moderately to conspicuously bicolorous, 30–48 cm long, 20–48 cm wide (1–1.5 times longer than wide), (0.8–1.8 times longer than petioles), upper surface dark green, drying dark gray to dark brown, semiglossy, lower surface drying dark yellow-brown to dark gray-brown, weakly glossy, moderately paler; anterior lobe 28–39 cm long, 8.5–14(17) cm wide (1.8–1.9 times longer than lateral lobes), rarely broadest at the base, usually narrowed toward the base (4–12 cm wide just above the base); sinus arcuate to broadly V-shaped; lateral lobes (7.5)15–22(27) cm long, 3–8(12) cm wide, broadest usually toward the apex, directed outward, broadly spreading (90–127° angle), broadly confluent with medial lobe 3.3–6.5 (rarely to 14) cm, acute; midrib broadly convex to flat-sunken above, convex, slightly paler than surface, drying blackened below; basal veins 8–10 per side, pinnately arranged along a stout medial rib; posterior rib not at all naked or rarely naked for 1–1.5 cm; primary lateral veins 5–6 per side (45–75° angle on median lobe), gradually curved to the margins, sunken above, convex, drying blackened below; interprimary veins weakly raised and darker than surface below; minor veins distinct, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1–3 per axil; peduncle (4.5)9–11(15) cm long; **spathe** (11)13–18 cm long, 8–10 mm diam. (1.4–1.6(2.4) times longer than peduncles), greenish white outside, greenish white to white within; spathe opening broadly at anthesis, convolute in only lower one-half of tube, barely or not at all constricted above the tube; spathe blade sometimes tinged white outside; spathe tube light green, sometimes tinged maroon at base outside; **spadix** held erect, not protruded forward, oblong to oblong-tapered, rounded to bluntly acute at apex, (9.5)11–15.5 cm long, broadest near the middle, constricted weakly above sterile staminate portion; pistillate portion pale green, oblong to oblong-tapered, 4.5–5.7 cm long, 8–10 mm diam. at apex, 8–12 mm diam. at middle, (5)11–13 mm wide at base; staminate portion 8–11 cm long; fertile staminate portion oblong-tapered, 8–13 mm diam. at base, (6)12–13 mm diam. at middle, 8–9 mm diam. ca. 1 cm from apex, usually broader than the pistillate portion; sterile staminate portion ca. 1 cm diam.; pistils 1.5–3 mm long, 1.1–1.8 mm diam., ovary 7–10-locular, (0.8)1.1 mm diam., with sub-basal placentation; ovules 1(2) per

locule, contained within transparent ovule sac, 0.6 mm long, usually shorter than funicle, style similar to style type B; style apex rounded; stigma button-like, subdiscoid, 1 mm diam., 0.2–0.4 mm high, covering center of style apex; thecae oblong to oblong-ovate, contiguous, sometimes divaricate. JUVENILE plants with petioles 8–10 cm long; blades oblong, rounded to weakly subcordate.

Flowering in *Philodendron angustilobum* has been recorded from the early dry season through the mid-wet season, including Februrary, March, May (the greatest number), and August, but too few collections exist to be certain of phenology.

Philodendron angustilobum ranges from Honduras (Olancho) to Panama, apparently being restricted to the Atlantic slope from Honduras to Costa Rica and ranging from near sea level to 680 m elevation. In Panama it has been collected on both slopes near the Continental Divide from 800 to 1430 m elevation, but a juvenile collection from near sea level in the Canal Area is probably also this species. It is known from *Tropical wet forest* and *Premontane wet forest* life zones.

Philodendron angustilobum is apparently a member of *P.* sect. *Tritomophyllum* [though M. Grayum (pers. comm.) believes it is closest to *P. ligulatum*, a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*]. This species is characterized by its moderately long internodes, spongy petioles, and 3-lobed blades, which dry blackened with broadly spreading lateral lobes that are much narrower and shorter than the medial lobes. It is superficially similar to *P. mexicanum* Engl., which has sagittate blades that dry green to brown and occurs typically in much drier habitats.

The sole Honduran collection might prove to represent another species or perhaps even a hybrid. It differs from material collected from Nicaragua, Costa Rica, and Panama in having the medial lobe broader, more triangular, and not at all constricted at the base.

Two collections (*Croat & Grayum 59933* and *Croat 67616*) from the same plant from southwestern Costa Rica near Golfito differ in having the posterior lobes less narrowed; they may prove to represent another species.

Additional specimens examined. COSTA RICA. **Cartago**: CATIE, near Quebrada Molina, SE of Florencia de Turrialba, ca. 680 m, 9°52′30″N, 83°40′W, *Grayum 3877* (MO). **Heredia**: Río Guacimal downstream from Monte Verde, 1300 m, *Grayum 5418* (CR, MO). **Puntarenas**: Coto Brus, Las Cruces Botanical Garden, near San Vito de Java, ca. 4000 ft., *Croat 32960* (MO); 6 km W of San Vito de Java, 1200 m, 8°49′N, 82°58′W, *57230* (MO); ca. 1 km NW of Golfito, 11 km SW of Interamerican Highway, <100 m, 8°11′N, 83°12′W, *Croat & Grayum 59933* (CR, F, K, MEXU, MO, US); Golfito–Villa Briceño, 3.1 mi. NW of center of Golfito, 30 m, 8°11′N, 83°12′W, *Croat 67616* (CM, CR, MEXU, MO). HONDURAS. **Olancho**: San Esteban–Bonito Oriental, along Río Olancho, 3.3 mi. SW of border with Colón Dept., along Río Grande, 350–400 m, 15°31′N, 85°42′W, *Croat & Hannon 64522* (CAS, CR, EAP, HNMN, K, MO, PMA, US). NICARAGUA. **Zelaya**: Río Sucio, 2 km E of Bonanza, 140 m, *Neill 4024* (MO). PANAMA. **Canal Area**: ca. 1 mi. E of Fort Sherman, <25 m, 9°19′N, 79°57′30″W, *Croat & Zhu 76283* (MO). **Chiriquí**: Cerro Colorado, 15.6 mi. above bridge over Río San Félix, 1330 m, *Croat 48439* (MO), 24 mi. above bridge over Río San Félix, 1430–1500 m, *48489* (MO), 800–1000 m, *33180* (MO); Gualaca–Chiriquí Grande, near Lago Fortuna, trail to Río Hornito, 8°45′N, 82°18′W, *76372A* (MO). **Coclé**: vic. of La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *67209* (CM, MO). **Panamá**: Cerro Campana, above Su Lin Motel, *14759* (MO, NY, SCZ).

Philodendron anisotomum Schott, Oesterr. Bot. Z. 8: 179. 1858. *Philodendron fenzlii* Schott var. *anisotomum* (Schott) Engl., in A. DC. & C. DC., Monogr. Phan. 2: 412. 1879. TYPE: Guatemala. Las Nubes, *Wendland 321* (lectotype, here designated, GOET). Figures 44, 53–56, 75.

Philodendron affine Hemsl., Diagn. Pl. Nov. Mexic.: 37. 1879. TYPE: Guatemala. Barranca Honda, Volcán de Fuego, 3800 ft., *Salvin s.n.* (holotype, K).

Philodendron dagilla Schott, Oesterr. Bot. Z. 5: 179. 1858. TYPE: Costa Rica. Cartago and Aguacate, *Oersted s.n.* (holotype, destroyed). Schott ic. 2592 (neotype, here designated).

Philodendron trisectum Standl., Publ. Field. Mus. Nat. Hist., Bot. Ser. 18: 137. 1937. TYPE: Costa Rica. Alajuela: La Palma de San Ramón, 1050 m, *Brenes 5762* (holotype, F).

Usually a hemiepiphytic vine or sometimes on rocks; stem appressed-climbing, green as juvenile, graying with maturity, minutely and densely striate, sap watery, unscented, leaf scars conspicuous, 8–10 mm long, 7–9 mm wide; internodes smooth, semiglossy, to 2.5 cm long, 4–10 mm diam., usually longer than broad, medium green to olive-green, epidermis thin, tan, peeling; roots olive green, smooth, few per node; cataphylls thin, semispongy, to 10 cm long, unribbed, bluntly or sharply 1-ribbed, green, drying pale yellow-green, deciduous. LEAVES erect to spreading; **petioles** 21–57 cm long, (2)3–9 mm diam., terete, moderately spongy, whitish toward apex, slightly flattened toward apex adaxially, surface dark green striate at base; **blades** triangular in outline, deeply 3-lobed, subcoriaceous, moderately bicolorous, long-acuminate at apex (the acumen apiculate, to 3 mm long), hastate at base, 20–35 cm long, 20–42 cm wide (0.8–1 times longer than wide), (0.6–1 times the

petiole length), upper surface dark green, semiglossy to glossy, drying dark brown to dark gray-green, lower surface semiglossy, paler, drying yellow-brown to yellow-green; anterior lobe oblong-lanceolate to oblanceolate, almost elliptic, 16–30 cm long, 7–15 cm wide (1–1.3(1.5) times longer than lateral lobes); lateral lobes broadly confluent 1–3(8) cm with medial lobe, 10–25 cm long, 3–8.7 cm wide, directed outward (90° angle from midrib), acute to bluntly acute; sinus arcuate; midrib ± flat to sunken, paler than surface above, broadly convex below; basal veins 4–7 per side, sometimes with last vein free to base, most veins coalesced 1.5–13 cm, 2 veins coalesced to 17 cm, drying reddish brown to yellowish brown; posterior rib naked; primary lateral veins 4–5 per side, departing midrib at a 50–60° angle, narrowly sunken above, convex below; interprimary veins weakly sunken and concolorous above, weakly raised and darker than surface below; tertiary veins visible, darker than surface below; minor veins fine, close, weakly visible to distinct below, arising from both the midrib and primary lateral veins but mostly from the midrib. INFLORESCENCES erect-spreading, 1 per axil; peduncle 5.5–19.5 cm long, 3–8 mm diam.; **spathe** 7.4–16.6 cm long (0.8–1.4(1.7) times longer than peduncle); spathe blade green to greenish white to creamy yellow, tinged with violet-purple outside, tinged with violet-purple, at least sometimes, with yellowish resin canals visible inside; spathe tube green outside, 4–6 cm long, 2–3.5 cm diam., dark violet-purple inside; **spadix** sessile; white, drying golden-yellow throughout, tapered, ± rounded at apex, 7.5–10.8 cm long, broadest near the base; pistillate portion pale green (post-anthesis), ellipsoid, 3.6 cm long, 1.3 cm diam. at apex, 1.2 cm diam. at middle, 6 mm wide at base; staminate portion to 8.4 cm long; fertile staminate portion white, ellipsoid, tapered at apex, 8 mm diam. at base, 5 mm diam. at middle, 5 mm diam. ca. 1 cm from apex, broadest at base, much narrower than the pistillate portion; sterile staminate portion tannish, 8 mm diam.; pistils (1.5)2.9–4.4 mm long, 1.7–2.3 mm diam., ovary (6)7–8-locular, (1)2.2–3.2 mm long, ovule sac 0.7 mm long, with sub-basal placentation; ovules 3 per locule, contained within translucent, gelatinous ovule sac, ca. 0.4 mm long, longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style similar to style type B; style apex flat; stigma discoid, 5–6 mm diam., 0.1 mm high, covering center of style apex; the androecium ± prismatic, margins irregularly 4–6-sided, 0.7–1.1 mm long; thecae oblong, 0.3 mm wide, ± divaricate; sterile staminate flowers irregularly 5–6-sided, 1 mm wide. INFRUCTESCENCE 9.5–16 cm long, peduncle to 14 cm long; spadix to 5.3 cm long, to 3 cm wide; berries orange, rhomboid; seeds 1–2(3) per locule, (16)21–22(29) per berry, light brown, 1.5–2 mm long, 0.5 mm diam., with weak constriction (nipple) opposite funicular end of seed.

Flowering in *Philodendron anisotomum* appears to be restricted to the rainy season in Central America. One collection was seen in flower in May but most are from July through December (the latter month is sometimes the beginning of the dry season in parts of Middle America). Immature fruits were collected from December through July, with mature fruits known only from March, April, and July.

Philodendron anisotomum ranges from Mexico to Costa Rica, at 30 to 1800 m elevation. In Mexico, the species ranges from Nayarit to Oaxaca and Chiapas mostly along the Pacific coast, but also occurs in Puebla (Ajenjibre) and Morelos (Cuernavaca). One collection, *Moore & Bunting 8874,* from near Córdoba in Veracruz state, appears out of range for the species.

Collections from Guatemala are few, but all are from the Pacific slope except one collection from Baja Verapaz between El Chol and Rabinal (*Croat & Hannon 63670*). In Honduras and Costa Rica, the species is nearly restricted to the Pacific slope. In Costa Rica the species occurs in *Premontane moist forest. Philodendron anisotomum* is a member of *P.* sect. *Tritomophyllum.*

This species is distinguished by its deeply three-lobed blades with frequently much smaller, falcate lateral lobes broadly confluent with the medial lobe.

Philodendron anisotomum is easily confused with *P. tripartitum* (Jacq.) Schott, which differs in having proportionately narrower medial lobes (mostly 3–3.5, rarely to 1.7 times longer than broad) with 4–9 prominently sunken primary lateral veins and lateral lobes typically directly more or less toward the apex. It has only one ovule per locule and white fruits. In contrast, *P. anisotomum* has medial lobes less than 1.5–2.8 times longer than broad with 2–4(5) weakly sunken primary lateral veins and usually much smaller lateral lobes typically directed outward, as well as 3 ovules per locule, and orange fruits.

Material from Nayarit (*McVaugh 13363, Moore & Bunting 8703)* is not only geographically isolated from populations in Puebla, Cuernavaca, and Oaxaca, but also differs morphologically by having much larger blades (medial lobe >23 cm wide) with the lateral lobes narrowly rounded rather than pointed.

Costa Rican collections differ in sometimes having two inflorescences per axil, rather than solitary inflorescences, which is more typical.

Philodendron dagilla Schott, published on the same page as *P. anisotomum*, was considered a synonym of *P. tripartitum* by Krause (1913), but it is clearly synonymous with *P. anisotomum*. Schott distinguished it from *P. anisotomum* by its longer, less spreading lateral lobes, but they are well within the norm.

Additional specimens examined. COSTA RICA. 1911, without locality, *Pittier & Durand 3090* (BR); *Worthen s.n.* (MO). **Alajuela**: San Pedro de San Ramón, 1075 m, *Brenes 4874(33)* (F); San Ramón, 1500–1600 m, *Tonduz 17719* (BM, K, P); San Ramón-Balsa, 2.3 km N of Río Balsa, 1050–1150 m, 10°11′N, 84°30′W, *Stevens 14193* (MO); ca. 5.7 km N of Quebrada Volio, 1100–1150 m, ca. 10°08′N, 84°29′W, *14165* (CR, MO); San Ramón–Balsa, 5.7 mi. N of San Ramón, 1200 m, *Croat 46837* (MO); San Ramón–Bajo Rodriguez, 940 m, *Croat 78892* (CR, INB, MO); San Ramón–San Lorenzo, 1 km S of Balsa, 1100 m, 10°10′N, 84°29′W, *Liesner & Judziewicz 14937* (CR, MO); 1–3 km E of San Ramón, ca. 1000 m, 10°05′N, 84°27′W, *Liesner 14198* (B, CR, MO); above Río San Luis, 15 km NW of San Ramón, 800 m, 10°14′N, 83°31′W, *Lent 3108* (F); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, 900 m, *Croat 43522* (MO); Zarcero region, ca. 100 m, *Smith A447* (MO); ca. 7.5 mi. N of Zarcero, ca. 1000 m, *Croat 43499* (MO); ca. 15 km N of Zarcero, 1350 m, *Williams et al. 29041* (F); along Rte. 9, ca. 2 km N of Cariblanco de Sarapiquí, 800 m, 10°17′N, 84°12′W, *Grayum et al. 8098* (MO); Atenas, near old Pan-American Highway, *Gentry 782B* (CR, MO); San Luis de Zarcero, Cantón Alfaro Ruiz, 1425 m, *A. Smith H1178* (F, MO); N of Carrizal, 1440 m, *Grayum 3085* (DUKE); Cantón San Carlos at Sucre, 975 m, *A. Smith H1669* (F, US); San Isidro de San Ramón, 1259 m, 10°04′46″N, 84°26′30″W, *Herrera 58* (AAU, M, MEXU, MO); Monteverde Biological Reserve, Río Peñas Blancas, 900 m, 10°18′N, 84°45′W, *Haber & Bello 7181* (MO); 1250–1350 m, 9°17′N, 84°84′W, *Burger et al. 10770* (CHAPA, CR); Río Peje, 4 km S of Ciudad Quesada, 960 m, *Lent 1274* (BM, CR, F, GH); Río Trojas, 2 km N of La Luisa, 1380 m, *1674* (CR, US). **Cartago**: Juan Viñas, 1300 m, *Carpenter 608* (US); S slope of Volcán Irazú, *Standley 36638* (US); *Stevens 48* (US). **Guanacaste**: La Cruz de Abangares, 1400 m, *Haber & Bello 2881* (MO); Monteverde, 1400 m, 10°22′N, 84°49′W, *Haber & Zuchowski 8734* (CR, ENCB, L, MO, QCA); 8 km NW of Monteverde, 1200 m, 10°22′N, 84°51′W, *Haber & Zuchowski 9518* (INB, MO). **Puntarenas**: Cordillera de Talamanca, foothills around Tres Colinas, 1800–1850 m, 9°07′N, 83°04′W, *Davidse et al. 25635* (MO); Cantón de Buenos Aires, Quebrada Dorora (tributary of Río Kuiyé), ca. 9 km NE of Ujarrás, 1500 m, 9°17′30N, 83°16′W, *Grayum 10275* (CAS, CR, INB, K, MO, US); Reserva Biológica Carara Estación Quebrada Bonita, 30 m, 9°46′N, 84°36′W, *Bello & Rojas 2286* (CR, INB, MO). **San José**: ca. 25 km N of San Isidro del General, along the Inter-American Highway, 1800 m, 9°29′N, 83°41′W, *Burger & Baker 10078* (CR, F); Finca Micos–Llano Limón, ca. 8.5 km by road W of Ciudad Colón, 550–650 m, 9°56′N, 84°18′W, *Grayum et al. 6096* (MO); San José, *Standley 47358* (US), ca. 1130 m, *41210* (US), *47334* (US), 1150 m, *33262* (US); 1.4 km NW of Brazil de Santa Ana, 800 m, *Taylor 17378* (NY, US); San Sebastián, S of San José, 1160 m, *Standley 49293* (US); San Pedro Montes de Oca–Curridabat, ca. 1200 m, *32830* (US), 1250 m, *41307* (US); Río María Aguilar, near San José, 1200 m, *38952* (US); Las Pavas, 1070 m, *36085* (US); camino de Hatillo, near San José, 1200 m, *32171* (US); Acosta, Z.P. Cerros de Escazú, Río Tabarcia, 1600–1700 m, 9°50′52″N, 84°04′40″W, *Morales 2745* (CR, MO); Valle del Candelaria, 1000–1050 m, *Morales & González 4596* (CR, INB); Santiago de Puriscal, *Echeverría 838* (F). EL SALVADOR. **Ahuachapán**: *Padilla 60297* (US), 1922, *297* (US), *60* (US); 2–3 mi. NE of Bridge Imposible, 1000–1250 m, *Croat 42162* (MO). **San Salvador**: Tonecatepeque, *Calderón 200* (US); 650–850 m, *Standley 19199* (GH, NY, US). GUATEMALA. **Alta Verapaz**: Cobán, ca. 1300 m, *Standley 90275* (F); Semococh, 17 km from Sebol, on Cobán Road, *Contreras 4714* (LL); 5 mi. N of Cobán, along Highway CA-14, 1300 m, *Croat 41406* (MO); 5 mi. S of Cobán, along Highway CA-14, 1300 m, *41364* (MO); San Juan Chamelco, *Wilson 41008* (F). **Baja Verapaz**: Mpio. Rabinal, El Chol–Rabinal, Highway 6, 8.7 mi. N of El Chol, 1330 m, 15°03′N, 90°29′W, *Croat & Hannon 63670* (GH, LL, MO, TEX). **Chiquimula**: Quezaltepeque, 1200–1500 m, *Steyermark 31198* (F). **Escuintla**: Escuintla–Santa Lucía Colz, Río Jute–Río Pantcaleon, *Standley 63390* (F); Río Burrión, NE of Escuintla, *89605* (F, MEXU). **Jalapa**: Los Chorras along Río Pinule, 1 mi. W of San Pedro Pinula, 1400 m, *Steyermark 32931* (F). **Jutiapa**: San José Acatempo–Río de los Esclanos, Cuesta de la Conora, 900–1200 m, *Standley 60616* (F). **Quezaltenango**: Reserve INDE, "Santa María," km 199, 1200–1300 m, 14°45′N, 91°32′W, *Croat & Hannon 63435* (B, BM, CM, MO, NY, US); Calahuaché, 1020 m, *Standley 67137* (F); below Santa María de Jesús, 1350–1380 m, *68386* (F); Finca Pirineos–Patzulín, 1200–1400 m, *86844* (F), *86918* (F). **Retalhuleu**: Río Coyote, 4 km W of Retalhuleu, 300 m, *87496* (F). **Sacatepéquez**: near Las Lajas, 1200 m, *58284* (F); Pueblo Nuevo, 750 m, *66976* (F). **San Marcos**: Finca Armenia, near La Trinidad, above San Rafael, 1100–1250 m, *Croat 40826* (MO); La Trinidad, ca. 2 km from Finca Armenia, above San Rafael, 1100–1250 m, *40864* (MO); Finca El Porvenir "Numero 6," Volcán Tajumulco, *Steyermark 37140* (F, MEXU); Volcán Tajumulco, above Finca Porvenir, 1300–1500 m, *37358* (F, US). **Santa Rosa**: El Molino, ca. 600 m, *Standley 78508* (F); Volcán Jumaytepeque, 6000 pp, *Heyde & Lux 4283* (CM, GH, NY, US). HONDURAS. **Olancho**: Río Olancho, Gualaco–San Bonito Oriental, 7.4 mi. NE of San Esteban, 540 m, 15°20′N, 85°42′W, *Croat & Hannon 64364* (MO, VEN). MEXICO. *Teas s.n.* (MO). **Chiapas**: 8.5 mi. NE of Escuintla, on gravel road to El Triunfo, 250 m, *Croat 43823* (MO); ca. 4 km N of Ovando Turquía, 450–850 m, *47575* (MO); Tapachula–Unión Juárez, at km 13.5, 1.3 mi. N of Trinidad, ca. 1000 m, *47212* (MO); San Fernando–Moravillas, near Lago Malpaso, 4–66 mi. NW of San Fernando, 840–940 m, 16°53′N, 93°06′W, *Croat & Hannon 65029* (CM, MO); Mpio. Angel Albino Corzo, along Río Cuxtepeques near Finca Gadow, 1270 m, *Breedlove 40162* (CAS, DS); Barr. Aguas Calientes, *Miranda 1740* (MEXU); finca between Finca Cuxtepeque and Finca Cabañas, 1100 m, *Breedlove & Daniel 71160* (CAS); Las Nubes, Guatimoc, *Miranda 1720* (MEXU); Cascada, Siltepec, 1800 m, *Matuda 38677* (MEXU); Motozintla de Mendoza–Huixtla, 15 mi. S of Motozintla de Mendoza, 900 m, *Croat 40764* (MO); Esperanza, Escuintla, *Matuda 17791* (MEXU, MO), *Matuda s.n.* (MO), *16661* (F, MEXU, MICH, MO), *17768* (F, GH, MEXU); Zacatonal, Acacoy-

agua, 1200 m, *18364* (MEXU); Cerro Ovando, 900–1050 m, *Croat 78479* (CHIP, CM, MO, NY); Escuintla, Turquía, *Matuda 17066* (F, MEXU); Mpio. Angel Albino Corzo, 1380 m, *Breedlove & Almeda 56917* (MO); 1380 m, *Breedlove & Strother 46700* (MO); Mpio. Mapastepec, Sierra de Soconusco, new unfinished road to Tuxtla Gutiérrez from Hwy. 200, (5.5 mi. NW of turnoff to Mapastepec), 6.5–8.5 mi. up road, 15°32′N, 92°48′W, *Croat & Hannon 63339* (B, BM, CM, MO, NY, PMA, US); Mpio. Villa Corzo, E base of Cerro Tres Picos, near Cerro Baul, 1500 m, *Breedlove 23968* (DS). **Jalisco**: 20–22 km S of Talpa de Allende, 1200–1450 m, *McVaugh 23308* (MICH). **Morelos**: near Cuernavaca, *Pringle 7015* (GH); Cuernavaca, *Rose & Hough 4438* (US). **Nayarit**: Tepic–Jalcocotán, near km 20, 700–800 m, *Moore & Bunting 8703* (BH); at km 15, ca. 900 m, *8694* (BH); ca. 4 mi. E of Jalcocotán on road to Tepic, 750 m, *McVaugh 13363* (MICH). **Oaxaca**: Oaxaca–Pochutla, along Highway 175, 55.1 mi. S of Miahuatlán, 21.9 mi. S of Suchixtepic, 39.7 mi. N of turnoff to Pluma Hildato, 1540 m, *Croat 46108* (MEXU, MO); Pinotepa Nacional–Tlaxiaco, along Highway 125, 5.8 mi. N of Putla de Guerrero, ca. 1000 m, *45904* (MO); Oaxaca–Pochutla, ca. 56 mi. S of Miahuatlán, 6.9 mi. N of turnoff to Pluma Hidalgo, 1480 m, *46116* (DUKE, F, MO). **Puebla**: Ajenjibre, *Bravo I-4516* (MEXU). **Veracruz**: Córdoba–Veracruz, Ejido San José de Gracia, below Peñuelo, *Moore & Bunting 8874* (BH).

Philodendron annulatum Croat, sp. nov. TYPE: Panama. Panamá: El Llano–Cartí road, 5 mi. from Pan American Hwy., virgin forest on steep slopes, along trail through forest (W side of road), 350 m, 9°17′N, 78°58′W, 16 July 1987, *Croat 67346* (holotype, MO 3609133; isotypes, B, CM, COL, CR, K, PMA, RSA, NY, US). Figures 57–60.

Planta hemiepiphytica, interdum epiphytica aut terrestris; internodia 1–4(11) cm longa, 1.5–3.5 cm diam.; cataphylla obtuse usque acute 2-costata aut incostata; petiolus subteres, 14–42 cm longus, subspongiosus cum annulo purpureo apice; lamina oblonga vel oblongo-ovata, subcordata, 24–73 cm longa, 8–29 cm lata; inflorescentia 1–2(3); pedunculus 3.6–11.5(17) cm longus; spatha 12.3–22 cm longa, lamina spathae extus alba vel viridalba, intus pallide viridis, tubo spathae extus viridi, intus viridi, striato rubello vel marronino basi; pistilla (5)7–8-locularia; loculi 1–2(4–5)-ovulati; baccae pallide virides vel albae.

Usually hemiepiphytic, sometimes epiphytic or terrestrial; stem appressed-climbing, sometimes creeping, to 1 m long, sap clear, sticky, sometimes black pepper-scented, leaf scars conspicuous, to 2.5 cm long, to 1.5 cm wide; internodes semiglossy, sometimes becoming matte, sometimes scurfy, 1–4(11) cm long, 1.5–3.5 cm diam., usually longer than broad, dark green to grayish or grayish green to brown, epidermis thin, drying brownish, irregularly ridged, frequently transverse fissured, cracking off; roots olive-green to brownish, slender, 0.6–100 cm long, to 3 mm diam., semiglossy, somewhat twisting, drying pale; cataphylls to 34 cm long, bluntly to sharply 2-ribbed (ribs to 5 mm high), green, densely short, dark green lineate or speckled, sometimes persisting as a rotting mass, eventually deciduous. LEAVES erect-spreading to spreading to weakly arching; **petioles** 14–42 cm long, ± terete, slightly spongy, medium green, obtusely flattened and sometimes with an obscure medial rib near apex adaxially, sometimes with adaxial margins erect, blunt, surface sparsely dark green short-lineate or unmarked, sometimes with a purple ring at apex, sheath 4–9.5 cm long; **blades** oblong to oblong-ovate, subcoriaceous, moderately bicolorous, semiglossy, subcordate at base, 24–73 cm long, 8–29 cm wide (2.5–3 times longer than wide), (ca. 1.7 times longer than petiole), margins moderately undulate, upper surface dark green, lower surface paler; anterior lobe 23.5–68 cm long, 11–27.5 cm wide (10.5–15.6 times longer than posterior lobes); posterior lobes usually narrowly rounded and somewhat spreading or broader than long, rarely cordulate and about as long as broad, 1.5–6.5 cm long, 4.1–11.6 cm wide; sinus open or closed with lobes overlapping; midrib flat to broadly convex, slightly paler than surface or concolorous above, convex to bluntly acute, mostly concolorous, sometimes minutely speckled, matte or slightly semiglossy below; basal veins (1)2–3(4) per side, usually all free to base, sometimes with 2 united for up to 2 cm; posterior rib usually absent, never naked when present; primary lateral veins 6–10 per side, departing midrib at a 60–70° angle, ± straight to the margins, obtusely sunken, paler than surface above, convex to weakly raised and darker than surface below; interprimary veins flat and darker than surface below; minor veins moderately distinct to ± obscure above and below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect to spreading, 1–2(3) per axil; peduncle 3.6–11.5(17) cm long, to 1.8 cm diam., somewhat flattened adaxially, green, sometimes tinged red, weakly lineate or unmarked; **spathe** 12.3–22 cm long (1.7–3.4 times longer than peduncle), to 3 cm diam. (when closed), oblong-linear, acute at apex, weakly constricted above the tube; spathe blade white to greenish white outside (opening 8.5 cm long, 5.5 cm wide), pale green, with orange resin canals inside; spathe tube green outside, 5–7 cm long, 2.3 cm diam., green, reddish to maroon or maroon-streaked at base inside; **spadix** stipitate to 4 mm long; white, 9–14.7 cm long, broadest above the middle, weakly constricted above sterile staminate portion; pistillate portion pale green, cylindrical, 2.9–5.4 cm long, 0.9–1.3 mm diam., weakly narrowed toward both ends; staminate portion 6.8–12.5 cm long; fertile staminate

portion white, cylindrical to clavate, weakly tapered at apex, (5–7)12–15 mm diam. at base, 8–16 mm diam. at middle, (4)6–9 mm diam. ca. 1 cm from apex, broadest at middle or at base; sterile staminate portion narrower or broader than pistillate portion, white, 4–15 mm diam.; pistils 1.5–2.1(3.5) mm long, ovary (5)7–8-locular, 0.8–1.2(2) mm diam., with sub-basal or basal placentation (or axile in *Croat 69250*); ovules 1–2(4–5) per locule, 1-seriate, contained within transparent ovule sac, 0.3–1.7 mm long, longer than or equal in length to funicle, style similar to style type B; style apex with the shallow depression completely covered by stigma; style boss sometimes shallow, broad; stigma discoid to button-like (brush-like), 0.5–1 mm diam., less than 0.3 mm high, drying with the crown button-shaped and flat to concave with moderately large stylar pores around its periphery; the androecium margins 5(4–6)-sided, somewhat scalloped, 2 mm long; thecae oblong, 0.5 mm wide, nearly contiguous, sometimes divaricate; sterile staminate flowers ± rounded. INFRUCTESCENCE (immature), pale yellow-green outside; spadix to 3 cm wide, pistillate spadix 8–11 cm long; berries pale green to white; seeds tan, 1 mm long, 0.6 mm diam. JUVENILE petioles sheathed nearly throughout; blades oblong, obtuse to rounded at base, lower surface sometimes maroon.

Flowering in *Philodendron annulatum* is vouchered by one collection in January, with the vast majority of post-anthesis collections made primarily between February through May, and single collections in August and October. Mature fruits have been seen for only June and July.

Philodendron annulatum is endemic to Panama, ranging from Veraguas (Santa Fe) to Panamá and San Blas (El Llano–Cartí Road), at 100 to 970 m elevation in *Tropical wet forest* and *Premontane rain forest.*

Philodendron annulatum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* The species is distinguished by having internodes somewhat longer than broad and drying light brown; usually sharply two-ribbed, deciduous cataphylls; somewhat spongy obtusely somewhat flattened petioles with a purple distal ring (hence the name "annulatum" from annulatus, meaning "having a ring"); oblong to oblong-ovate, subcordate blades; and one to two inflorescences per axil with the spathe blade white and the tube green outside (usually colored or tinged red to maroon within).

Philodendron annulatum is most easily confused with *P. ligulatum* Schott. *Philodendron correae* Croat also has narrow, usually cordulate leaf bases and petioles with a purplish annular distal ring. Both differ from *P. annulatum* in having narrower blades broadest at or above the middle and narrowest just above the narrowly cordulate base. Alternatively, blades of *P. annulatum* are broadest at or near the base. *Philodendron annulatum* can also be confused with narrow-leaved representatives of *P. sagittifolium.* That species differs in having typically purple-spotted petioles (and often midribs) that lack a purplish distal ring.

Additional specimens examined. PANAMA. **Coclé**: 46 km N from Penonomé on road to Coclesito, 100 ft., *Hammel 1698* (MO); El Copé region, Alto Calvario, on Continental Divide, 5.2 mi. above El Copé, 930 m, *Croat 49186* (COL, K, MO); Alto Calvario above El Copé, ca. 6 km N of El Copé, 710–800 m, 8°39′N, 80°36′W, *68728* (AAU, CAS, K, L, M, MEXU, MO, PMA, TEX, US); 860 m, *Folsom 1257* (MO); 4.1 mi. N of El Copé, 680–770 m, 8°39′N, 80°36′W, *74831* (CAS, CM, F, MO, PMA), *74855* (L, MO, PMA); E of sawmill along old logging road, 2600 ft., *Hammel 4076* (MO); 4.5 mi. N of El Copé, 2.5 mi. N of Escuela Barrigón, 580–740 m, 8°38′N, 80°36′W, *Croat 67524* (AAU, COL, MO, US); El Valle region, vic. of La Mesa, N of El Valle de Antón, along E edge of Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67225* (COL, MO, US); La Mesa, above El Valle, *Croat 13467* (MO, SCZ); 775 m, 8°36′N, 80°07′W, *74803* (AAU, CAS, MO, PMA); 800 m, *Croat & Zhu 76676* (MO). **Colón**: Río Guanche, ca. 1 km upstream from bridge at the Colón–Portobelo Road, 100 m, 9°30′N, 79°39′W, *Croat 75191* (CM, MO, TEX); Río Iguanita, ca. 3 km above the bridge on Portobelo road, <100 m, 9°27′N, 79°40′W, *49760* (CM, MO). **Panamá**: El Llano–Cartí, 10 mi. from Pan-American Highway, 350 m, 9°14′N, 79°W, *Knapp et al. 4727* (MO); 450 m, 9°14′N, 79°W, *Knapp & Huft 4431* (MO); 7.5 km N of highway, *Folsom 2555* (MO); 5–6 mi. N of highway, 350–375 m, *Croat 34762* (MO); ca. 16–18 km from highway, 400 m, *Tyson & Nee 7344* (F, MO), *7357* (MO, US); 4 mi. from highway, *Croat 33731* (MO, NY); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *68696* (CM, KYO, MO, PMA, RSA); Cerro Jefe region, 750–800 m, 9°14′N, 79°22′W, *67088* (MO); 850 m, *67054* (MO); ca. 0.5 mi. below tower, 700–800 m, 9°15′N, 79°30′W, *Thompson 4789* (MO); 800 m, *Sullivan 211* (MO); 21 km above Pan-American Highway, ca. 600 m, *Croat 35889* (MO); 4.6 km beyond peak on road to Altos de Pacora, 26.3 km from the Inter-American Highway, 600 m, *35895* (MO); 0.8 mi. beyond turnoff to Altos de Pecora, 970 m, 8°43′N, 82°17′W, *Croat & Zhu 76620* (MO); Río Teralde, on road 8 km from Pan-American Hwy., 400 m, 9°08′N, 79°W, *Knapp 1825* (MO). **San Blas**: El Llano–Cartí Road, 14 mi. N of Pan-American Highway, 300 m, 9°15′N, 79°W, *Croat 69247* (CM, DUKE, MO, TEX), *69250* (CM, MO, NY); 14.5 mi. N of highway, 350 m, 9°15′N, 79°W, *McPherson 9508* (MO, PMA); 10.1 mi. N of highway, 300 m, *Croat & Zhu 76540* (MO); 1 mi. S of Nusagandi, 9 mi. N of Interamerican Highway, 350 m, 9°20′N, 79°W, *Croat & Zhu 77013* (MO); *76568* (MO, US); *76569A* (MO); 10.1 mi. N of main highway, 300 m, 9°20′N, 79°W, *Croat & Zhu 76540* (MO); near Nusagandi, along Sendero Nusagandi, 300–350 m, 9°15′N, 79°W, *McPherson 10756* (MO); 1–5 mi. N of Nusagandi, 250–300 m, 9°16′N, 79°W, *Thompson 4661* (CM). **Veraguas**: Santa Fe region, Santa Fe–Río San Luis, past Escuela Agrícola

Alto de Piedra, 8 mi. N of school, 450 m, 8°33′N, 81°08′W, *Croat 66954* (K, MO, NY, PMA, QCA); 0.2 mi. beyond fork in road at Escuela Agrícola Alto Piedra, 750 m, *33971* (MO).

Philodendron antonioanum Croat, sp. nov. TYPE: Panama. Veraguas: vic. of Santa Fe, along road between Alto Piedra and Calovébora, 0.5 mi. N of Alto Piedra, on slopes of Cerro Tute, Parque Nacional Cerro Tute, 1030 m, 15 July 1994, *Croat & Zhu 76909* (holotype, MO–4619868–9, MO–4619871–2; isotypes, B, CAS, COL, CR, F, GH, K, MEXU, MO, NY, PMA, SCZ, US, VEN). Figures 61–64.

Planta hemiepiphytica; internodia brevia, 4–7 cm diam.; cataphylla rubra, acute 2-costata, persistentia ut fibrae tenues; petiolus 28–91 cm longus, obtuse complanatus adaxialiter; lamina ovata, 26–86 cm longa, 18–57 cm lata, nervis primariis lateralibus 5–6 utroque; inflorescentia 2; pedunculus 6–7 cm longus; spatha 15–16 cm longa; lamina spathae extus viridalba, intus alba suffusa rubella in dimidio inferiore; tubo spathae in superficibus ambabus marronino; pistilla 5-locularia; loculi 25–30-ovulati.

Hemiepiphytic; larger stems drying reddish brown, smooth, and coarsely striate at nodes, smaller stems drying light yellow-brown, glossy, and finely longitudinally ribbed, finally dark brown and transversely finely cracked; internodes short, 4–7 cm diam., broader than long; roots to 30 cm long, numerous per node, drying reddish brown, weakly glossy, and somewhat ridged; cataphylls 35–39 cm long, sharply 2-ribbed, red, broadly sulcate abaxially, persisting as pale brown fibers densely clothing the entire apex of the stem with tiny fragments of reddish brown epidermis persisting among the fibers; **petioles** 28–91 cm long, 1.5–2 cm diam., subterete, obtusely flattened adaxially, weakly 1-ribbed near apex, broadly and obtusely sulcate, to 3.5 cm diam. near base, dark green (reddish brown when young), drying reddish brown and matte, surface moderately glossy, prominently striate-lineate throughout; **blades** broadly ovate, moderately coriaceous, bicolorous, semiglossy, 26–86 cm long, 18–57 cm wide (1.2–1.5 times longer than wide), margins broadly and sparsely undulate, upper surface drying dark brown to gray-brown, lower surface drying reddish brown; sinus hippocrepiform to obovate, 4–18 cm deep; midrib flat and slightly paler than surface, drying convex and darker than surface above, convex, sometimes tinged reddish, drying obtusely angular, grayish brown, and sparsely short pale-lineate below; basal veins 7 per side, with the first and second free to base, the third through sixth veins coalesced to 7 cm, posterior rib barely naked near the base, weakly curved; primary lateral veins 5–6 per side, departing midrib at a 40–50° angle, drying reddish brown below, obtusely and deeply sunken, concolorous, drying raised and somewhat darker above, convex, ± concolorous, drying concolorous, matte below; minor veins moderately distinct, drying prominulous above and below, arising from both the midrib and primary lateral veins, secretory canals appearing but not obvious below; "cross-veins" numerous, ± transverse. INFLORESCENCES 2 per axil; peduncle 6–7 cm long, 1.5 cm diam., magenta, conspicuously white-striate toward the apex; **spathe** 15–16 cm long, weakly constricted midway, weakly glossy, moderately coriaceous, drying reddish brown on both surfaces, acuminate at apex; spathe blade greenish white outside, white, tinged reddish in lower half inside; spathe tube inflated, dark maroon outside, to 7 cm long, 5.8 cm diam., dark maroon inside; **spadix** 15 cm long; pistillate portion 3.5–5 cm long in front, 3.3–3.7 cm long in back, 2–2.5 cm diam. at apex, 2.3–3 cm wide at base; staminate portion 9–11.7 cm long; fertile staminate portion gradually tapered toward apex; sterile staminate portion 2.5–2.6 cm diam.; pistils 3.2–3.5 mm long, creamy brown, ovary 5-locular, ca. 0.4 mm long, with parietal placentation; ovules 25–30 per locule, 2–3-seriate; funicle ca. 0.2 mm long, style 1 mm diam., similar to style type B; style apex flat, with small depressions; stigma 1.3–1.5 mm diam., 0.4 mm high, covering entire style apex; the androecium margins sharply 4–6-sided, 0.6–1.2 mm diam. at apex; sterile staminate flowers rounded to bluntly 4–6-sided, larger toward the base, 0.6–2.8 mm wide.

Flowering in *Philodendron antonioanum* probably takes place in the early rainy season. Two fertile collections have been seen, one with immature fruits in June and one post-anthesis in July.

Philodendron antonioanum is endemic to central Panama and known only from the type locality at Cerro Tute and at El Copé at 800 to 1200 m elevation in *Tropical Lower Montane rain forest. Philodendron antonioanum* is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* The species is distinguished by its red, sharply two-ribbed cataphylls, which persist as fibers; its subterete petioles longer than the blades; broadly ovate reddish brown drying blades with 5–6 primary lateral veins; and by the stout inflorescences with scarcely constricted spathes having the tube magenta on both surfaces.

Philodendron antonioanum is most easily confused with *Philodendron tysonii,* a species with which it may occur. Both species occur at higher

elevations, and have subterete petioles longer than blades, large, ovate, glossy blades, and red or reddish cataphylls persisting as fibers. *Philodendron tysonii* differs in having mostly unribbed cataphylls and blades with usually 6–10 primary lateral veins and with the upper surfaces drying usually more or less blackened and smooth, in contrast to blades with 4–6 primary lateral veins and with upper surfaces drying gray-green with prominulous crossveins as in *P. antonioanum*. In addition, *P. tysonii* has more prominently pedunculate inflorescences with green spathes, which are merely tinged red on the tube outside and are proportionately more slender and more constricted above the tube rather than being dark magenta on the tube and barely constricted above the tube as in *P. antonioanum*. Finally, the species differ in the nature of ovules, with *P. tysonii* having ovaries (5)6–8(9)-locular with subbasal placentation and (4)5–7 ovules per locule borne in an envelope, while *P. antonioanum* has ovaries 5-locular with parietal placentation and about 30 ovules per locule not borne within an envelope.

The species is named in honor of Thomas Antonio of the Chicago Botanic Garden, who was resident botanist in Panama for the Missouri Botanical Garden and who first collected the species in June 1980.

Additional specimens examined. PANAMA. **Coclé**: Alto Calvario above El Copé, ca. 6 km N of El Copé, 710–800 m, 8°39′N, 80°36′W, *Croat 68766A* (MO); 930 m, *49197* (CM, M, MO); along Continental Divide, 900–1000 m, 8°39′N, 80°36′W, *75051* (MO). **Veraguas**: vic. of Santa Fe, along road between Alto Piedra and Calovébora, 0.5 mi. N of Alto Piedra, on slopes of Cerro Tute, 1150 m, *Antonio 4945* (MO, PMA).

Philodendron aromaticum Croat & Grayum, sp. nov. TYPE: Costa Rica. Limón: 3.5 airline km S of Islas Buena Vista in the Río Colorado, 16 airline km SW of Barra del Colorado, 10–120 m, 10°39′N, 83°40′40″W, 15–16 Sep. 1986, *Davidse & Herrera 31212* (holotype, MO–3582209–10; isotype, US). Figures 66–68.

Planta plerumque epiphytica; internodia 2–3 cm longa, 1.5–3.5 cm diam.; cataphylla acute 2-costata, decidua; petiolus subteres, 33.5–66 cm longus, subspongiosus; lamina ovato-cordata, 33–55 cm longa, 17–26 cm lata, in sicco canoviridis supra, viridis vel brunneiviridis infra; inflorescentia 1; pedunculus 4.5–9.4 cm longa; spatha 15–20 cm longa, lamina spathae extus atriviridi, intus pallide marronina vel alba; tubo spathae atrimarronino; pistilla 9–10(11)-locularia; loculi 2–3-ovulati.

Usually epiphytic, sometimes hemiepiphytic (often occurring high in canopy), rarely terrestrial (accidentally); stem usually appressed-climbing, creeping, brownish, sap sweet, turpentine- to burseraceous-scented; internodes weakly glossy, minutely striate longitudinally, 2–3 cm long, 1.5–3.5 cm diam., usually broader than long, dark to medium green, drying brown, epidermis fissured longitudinally; roots moderately few, drying reddish brown; cataphylls sharply 2-ribbed, D-shaped, deciduous, margins sharply raised. LEAVES erect-spreading to spreading; **petioles** 33.5–66 cm long, ± terete, somewhat spongy, dark green, obtusely to weakly flattened adaxially, surface weakly glossy, not noticeably marked, drying 8–15 mm diam., usually greenish dark brown; **blades** ovate-cordate, subcoriaceous, glossy, weakly bicolorous, acuminate to long-acuminate at apex (the acumen inrolled, 7–11 mm long), cordate at base, 35–55 cm long, 17–26 cm wide (2.1 times longer than wide), (0.8–1 times longer than petiole), margins weakly undulate; upper surface dark green, semiglossy, drying gray-green, lower surface glossy to semiglossy, paler, drying green to brownish green; anterior lobe 30.5–41 cm long, 16–26 cm wide (2.6–2.9 times longer than posterior lobes); posterior lobes 10.5–15.8 cm long, 7–13 cm wide, rounded at apex; sinus spathulate, 12 cm deep; midrib flattened, slightly paler than surface above, raised to convex, paler than surface below; basal veins 5–6 per side, with none or rarely 1 free to base, two to three veins coalesced 2.7–5.5(6.3) cm; posterior rib naked for 4 cm; primary lateral veins 5–7 per side, departing midrib at a 70–80° angle, straight to the margins, weakly and narrowly sunken above, convex and paler than surface below; minor veins moderately obscure to clearly visible below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 4.5–9.4 cm long, 0.08–0.15 cm diam., green, weakly striate; **spathe** semiglossy, 15–20 cm long (2.1–3.3 times longer than peduncle), constricted above the tube, dark green throughout, pale maroon to white inside; spathe tube oblong-ellipsoid, weakly wrinkled longitudinally outside, 6–9 cm long, dark maroon, suffused onto blade inside; **spadix** sessile; greenish white to white throughout, oblong, 12–16.9 cm long; pistillate portion creamy white to pale green, cylindrical, 5–13 cm long, 6–12 mm diam. at apex, 12 mm diam. at middle, 5–10 mm wide at base; staminate portion 7–11 cm long; fertile staminate portion white, ellipsoid, 1 cm diam. at base, 1.4 cm diam. at middle, 6 mm diam. ca. 1 cm from apex, broadest at the middle, slightly broader than the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, white, 1.5 cm diam.; pistils 3 mm long, 1.1–1.3 mm diam., ovary 9–10(11)-

locular, 1.8 mm long, 1.2 mm diam., with sub-basal placentation; ovules 2–3 per locule, contained within translucent or transparent ovule sac, 0.3 mm long, ± equal in length to funicle, style similar to style type B; style crown about as broad as ovary; central style dome well developed; style apex with central domes; stigma discoid, weakly lobed, 1.1 mm diam., 0.2–0.3 mm high, covering entire style apex, depressed medially; the androecium margins mostly 5-sided, sometimes 4–6-sided; thecae oblong to ovate, 0.4 mm wide.

Flowering phenology in *Philodendron aromaticum* is unclear since too few collections exist, although present collections might suggest bimodality. Post-anthesis collections have been made in September, October, and in February. Immature fruiting collections have also been made in the same months, and mature fruiting collections have been made in September.

Philodendron aromaticum is endemic to the Atlantic slope of northwestern Costa Rica from sea level to 360 m elevation in a *Tropical wet forest* life zone.

Philodendron aromaticum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. The species is characterized by its thick, bare, short internodes; sharply two-ribbed, deciduous cataphylls; moderately spongy, obtusely flattened petioles longer than the blades; ovate-cordate blades drying gray-green on the upper surface and green to brownish green below; and by its solitary inflorescence with a short peduncle and green spathe, which is maroon on the tube within. Also characteristic is the mucilaginous, aromatic sap of the petioles (hence the name).

Philodendron aromaticum is most easily confused with *P. sagittifolium*, but that species typically has more elongate blades, which dry usually reddish brown; basal veins free or at least not forming a posterior rib that is naked at the sinus; and often more than a single inflorescence per axil. In contrast, *P. aromaticum* has blades with a prominent posterior rib naked along much of the sinus.

Additional specimens examined. COSTA RICA. **Cartago:** Turrialba, *Dress 6331* (BH; cultivated). **Heredia**: San José–Pto. Viejo, vic. of Chilamate, 11.6 mi. N of Cariblanco, 100 m, 10°27′N, 84°05′W, *Croat 68382* (CAS, CR, F, G, L, M, MO); La Selva Field Station, Puerto Viejo de Sarapiquí, along El Surá Trail, 100–150 m, *44315* (MO); ca. 100 m, *Folsom 8963* (DUKE); *9438* (DUKE); *Grayum 2686* (DUKE); *Hammel 10733* (DUKE); *Croat 61214* (MO). **Limón**: 2–3.5 airline km SSE of Islas Buena Vista in the Río Colorado, 14 airline km SW of Barra del Colorado, 10–120 m, 10°40′N, 83°40′W, *Davidse & Herrera 31136* (CR, MO, US); Cerro Coronel, 10–80 m, 83°39′30″W, 10°40′30″N, *31481* (CR, MO); 20–170 m, 10°41′N, 83°38′W, *Stevens 23764* (MO); 2 km W of Río Toro Amarillo, on road W from Guápiles, 275 m, 10°13′N, 83°50′W, *Thompson & Rawlins 1197* (CM); Río Sierpe, 5 km NE of La Aurora, Guápiles, 30 m, 10°22′N, 83°31″W, *Robles 2189* (CR); *2238* (CR, MO); Río Frío–Limón, vic. of Río Blanco, W of Guápiles, 360 m, 10°12′N, 83°49′W, *Croat 68423* (B, CR, K, MO); Refugio Nacional de Vida Silvestre, Río Chirripocito–Río Sardina, 12 m, 10°38′N, 83°45′W, *Grayum 9778* (CR, MO).

Philodendron auriculatum Standl. & L. O. Williams, Ceiba 3: 108. 1952. TYPE: Costa Rica. Puntarenas: Esquinas forest preserve, Esquinas Experiment Station, region between Río Esquinas and Palmar Sur de Osa, 60 m, *Allen 5697* (holotype, EAP; isotypes, F, US). Figures 12, 20, 23, 65, 69–72.

Usually epiphytic, sometimes epilithic, rarely terrestrial; stem appressed-climbing, creeping, leaf scars conspicuous, 2.5–3 cm long, 2.5–3.5 cm wide; internodes short, scurfy, 1–4 cm long, 1.5–5.5 cm diam., usually broader than long, dark green, drying becoming light tan with age; roots purplish maroon at base, brownish green or yellow at apex, pubescent, tapered, slender, to 27 cm long, 3–4 mm diam., few per node, sometimes emerging through the cataphylls at the nodes; cataphylls subcoriaceous, sometimes moderately spongy, 13–50 cm long, sharply 2-ribbed, pale green, drying brown, several persisting intact, eventually deciduous, emarginate with subapical apiculum at apex. LEAVES mostly erect or erect-spreading; **petioles** 24–53 cm long, 7–23 mm diam., erect to spreading, subterete, ± spongy, green, somewhat flattened at base adaxially, rounded abaxially, surface short, dark, green-lineate and with dark green ring at apex; **blades** usually oblong-oblanceolate, rarely oblong-elliptic, broadest from middle to above middle, with narrow auriculate lobes, subcoriaceous, bicolorous, acuminate at apex (the acumen inrolled), usually narrowly cordulate or auriculate at base, 37.5–75 cm long, 9–23 cm wide (3.3–4.2 times longer than wide), (1.4–1.6 times longer than petiole), broadest at the middle, upper surface dark green, drying pale yellow-green, semiglossy, lower surface slightly paler green, semiglossy; sinus 7–14 mm deep; midrib broadly convex at base becoming flattened toward the middle, eventually weakly sunken at apex above, green, with dark green lineations, midrib convex at base, eventually narrowly convex at apex below, green-striate, paler than surface; primary lateral veins 7–10(11) per side, departing midrib at a 80–85° angle, ± straight to the margins, sunken, concolorous above, raised to round-raised, paler than surface below; interprimary veins numerous, usually as conspicuous as

primary lateral veins; minor veins arising mostly from the midrib, fewer from the primary lateral veins; lesser veins obscure above, fine, moderately conspicuous and darker than surface below. INFLORESCENCES ± erect, 1–2 per axil; peduncle 7–11.3 cm long, 9–11 mm diam., medium to pale green, unmarked, semiglossy; **spathe** erect-spreading, subcoriaceous, 13–14.5 cm long (1.2–1.8 times longer than peduncle), weakly constricted midway (6 cm above base); spathe blade broadly flattened, curved weakly forward, pale greenish outside, to 9 cm long (opening elliptic in face view, 5.5 cm wide), pale green, heavily suffused with red (B & K Red-Purple 3/10) throughout inside; spathe tube oblong-ellipsoid, medium to dark green outside, densely short lineate throughout outside, 6 cm long, 3.5 cm diam., red to maroon (B & K Red-Purple 3/10) at base, weakly so toward apex inside; **spadix** oblong (weakly tapered or weakly clavate), 11–24 cm long, broadest usually at the middle; pistillate portion medium to dark green, tapered toward the apex, 2.3–4.2 cm long, 2.7–4.3 cm long in front, 2.4–2.7 cm long in back, 8–12 mm diam. at apex, 9–15 mm diam. at middle, 5–7 mm wide at base; staminate portion 9.5–12 cm long; fertile staminate portion weakly tapered or weakly ellipsoid, 8–16 mm diam. at base, 10–16 mm diam. at middle, 6–10 mm diam. ca. 1 cm from apex, broadest at the middle or ± uniform, broader than or as broad as the pistillate portion, as broad as the sterile portion; sterile staminate portion broader than or as broad as the pistillate portion; sterile staminate portion 0.7–1.5 cm diam.; pistils to 2.6 mm long, to 1.6 mm diam.; ovary 5–7(8–9)-locular, 0.7–1.2(2.1) mm long, (0.7)1.1–1.3 mm diam., with sub-basal placentation; ovules (3)4 per locule, 1-seriate (or in 2 series of 2), contained within translucent ovule sac, if present, 0.2–0.4 mm long, usually longer than funicle, style similar to style type B; style crown usually as broad as ovary; stigma discoid, 0.7–1 mm diam., 0.1–0.3 mm high, covering entire style apex; the androecium margins 4–6-sided and scalloped, 1–2.3 mm diam. at apex; thecae oblong (elliptical, slightly obovate); sterile staminate flowers irregularly rounded to bluntly 5-sided, 2.3–3 mm long, 1–1.5 mm wide, white. INFRUCTESCENCE with berries orange.

Flowering phenology in *Philodendron auriculatum* is unclear, but possibly flowering is initiated in the late rainy season. Only a single flowering collection exists (October), but there are a modest number of collections collected post-anthesis during the dry season and early rainy season (January through June). A single mature fruiting collection was made in January.

Philodendron auriculatum occurs only in southwestern Costa Rica on the Pacific slope from San José and Puntarenas Provinces (as far west as Carara), ranging from near sea level to 1200 m elevation in *Tropical wet forest* life zones.

Philodendron auriculatum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. This species is characterized by short internodes, sharply two-ribbed, deciduous cataphylls, moderately long, markedly spongy, somewhat flattened petioles (averaging slightly shorter than the blades), oblong-elliptic to oblong-oblanceolate, pale yellow-green-drying blades, which are usually narrowly cordulate at base, and one to two greenish inflorescences, which are red to maroon within at base.

Philodendron auriculatum is probably most closely related to *P. pseudauriculatum* Croat, which ranges along the Atlantic slope of Central America from Nicaragua to Panama and also on the Pacific slope of Panama near the Continental Divide (as well as the Serranía de Cañasas and Serranía de Pirre). That species differs in its usually darker gray-green-drying leaf blades with a dark green ring at the apex of the petiole, and in having the leaf base acute, rounded, or broadly subcordate at base (lacking the narrow auriculate lobes so common for *P. auriculatum*). In addition, *P. pseudauriculatum* has the whitish spathe clearly demarcated from the contrasting green peduncle. In contrast, *P. auriculatum* has a yellowish green spathe that is not at all demarcated from the peduncle.

Additional specimens examined. COSTA RICA. **Puntarenas**: near Inter-American Highway in vic. of Piedras Blancas, *Croat 32956* (CR, MO); hills N of Palmar Norte, along trail to Jalisco, 50–700 m, *Croat 35205* (MO); cove at NE base of peninsula, 3 km S of Puerto Quepos, 0 m, 9°24′N, 84°10′W, *Grayum & Sleeper 6612* (CR, K, MO, US); El General Valley, along Río Sonador, near Pan-American Highway, 600 m, *Williams et al. 28808* (F); along the Río Cacao above Pan-American Highway, 900 m, *Williams et al. 28687* (F); Las Cruces Tropical Botanical Garden, Cantón Coto Brus, 6 km W of San Vito de Java, 1200 m, 8°49′N, 82°58′W, *Croat 57268* (MO); 8.8 mi. N of Villa Neily, 1010 m, *66171* (MO); Osa Península, vic. Boscosa, *Croat & Hannon 79297* (INB, MO); Esquinas Ridge, 150–250 m, *Gómez 19677* (MO, NY, RSA, US); Rincón de Osa, *Liesner 1819* (F, MO); ca. 5 km W of Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Liesner 7298* (F, MO, PMA); *7306* (CR, F); 50–200 m, 8°42′N, 83°31′W, *Burger & Gentry 8978* (CR, F); 8°42′N, 83°31′W, *Aguilar 1507* (INB, MO); Piedras Blancas–Rincón, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67691* (MO); Quebrada Aparicio–Quebrada Aguabuena, Rincón de Osa, 200–400 m, 8°42′N, 83°31′W, *Grayum et al. 4013* (MO); Chacarita–Rincón de Osa, ca. 6 km W of Inter-American Highway at Chacarita, 100 m, 8°45′N, 83°18′W, *Croat & Grayum 59730* (CM, CR, K, MO, SAR); Parque Nacional Corco-

vado, Sirena, 0–150 m, 8°27–30′N, 83°33–38′W, *Kernan 25* (CR, MO); Estación Sirena, S of Río Sirena along Río Camaronal, 0 m, 8°28′N, 83°35′W, *Knapp 2188* (CR, L, MO, US); Talamanca Range, Pacific slope, forested foothills of mountains E of Quepos, 150–250 m, 9°29′N, 84°03′W, *Burger et al. 10603* (F, MO). **San José**: Puriscal, Z.P. La Cangreja, 300 m, *Morales et al. 3239* (CR, INB); Carara–El Sur de Turrubares, 280–370 m, 9°45′30″N, 84°32′W, *Grayum 10445* (CR, INB, MO).

Philodendron bakeri Croat & Grayum, sp. nov. TYPE: Costa Rica. Guanacaste: W slope of Cerro Nubes, ca. 2 km E of Silencio de Tilarán, large patch of remnant primary forest, 900 m, 10°28′N, 84°53′W, *Grayum, Herrera & Sleeper 4992* (holotype, MO–3392250; isotypes, CR, DUKE). Figures 77, 78.

Planta hemiepiphytica; internodia pleurumque longiora quam lata, (2)7–9 cm longa, (0.7)1–1.5 cm lata; cataphylla 5–10 cm longa, acute 1-costata aut raro vel acute 2-costata, decidua; petiolus subteres, 4–12 cm longus, 2–4(6) mm diam.; lamina plus minusve oblonga aut anguste oblonga vel oblanceolata, basi cuneata vel rotundata, 12–25.5 cm longus; inflorescentia 1; pedunculus 2.6–5.2 cm longus, 2–5 mm diam.; spatha 7–11.5 cm longa; lamina spathae extus pallide viridi vel crema suffusa rubra vel marronina, intus viridi vel albida suffusa rubra; tubo spathae intus atrimarronino, rubro aut carmesino; pistilla 5–8(10)-locularia; loculi 1(2)-ovulati; baccae aurantiaceae.

Hemiepiphytic; stem scandent, slender, to 1.5 m long; internodes (2)7–9 cm long, (0.7)1–1.5 cm diam., usually longer than broad, medium green, ± matte, becoming light brown, epidermis fissured minutely longitudinally upon drying; roots dark brown, thin; cataphylls subcoriaceous, 5–10 cm long, unribbed, bluntly to sharply 1-ribbed or rarely sharply 2-ribbed, green to reddish or maroon, deciduous, narrowly rounded at apex, margins clear. LEAVES spreading; **petioles** 4–12 cm long, 2–4(6) mm diam., spreading, subterete to C-shaped, sometimes tinged reddish, sometimes maroon at base, obtusely somewhat flattened or bluntly sulcate adaxially, rounded abaxially, surface semiglossy, with narrow purple ring at apex; sheathing 2.7–3.2 cm long, sheathing to ca. 2 cm but for ½ to ⅓ of its petiole length when subtending inflorescences; geniculum subterete, maroon, 2.7–4 cm long, darker than petiole; **blades** ± oblong or narrowly oblong to oblanceolate, moderately coriaceous, acuminate to long acuminate, sometimes acute at apex (the acumen sometimes short apiculate, 1–3 mm long), cuneate to rounded at base, 12–25.5 cm long, (2.7)4–10 cm wide (2.5–3 times longer than wide), (2–3 times longer than petiole), margins thin, narrow, reddish, upper surface drying reddish brown, semiglossy, lower surface weakly glossy; midrib flat to sunken, slightly paler than surface above, narrowly convex, reddish violet below; basal veins lacking; posterior rib lacking; primary lateral veins 3–4 per side, departing midrib at a 45–55° angle, ascending to the apex, inconspicuous or slightly sunken above, not distinct below; tertiary veins visible, darker than surface; minor veins obsurely visible to moderately distinct, fine, close, arising from midrib only; secretory ducts usually obscurely visible on lower surface of dried blade. INFLORESCENCES 1 per axil; peduncle 2.6–5.2 cm long, 2–5 mm diam., obscured by petiole sheath; **spathe** moderately coriaceous, 7–11.5 cm long (2.2–2.7 times longer than peduncle), scarcely or not at all constricted, pale green to cream, often tinged lightly or heavily with reddish lineations, sometimes solid red or maroon, or with red speckles or lines (rarely seen in Panamanian specimens), green to whitish, suffused with red inside; resin canals appearing medially, especially near the constriction; spathe tube cylindrical, semiglossy outside, 4–5 cm long, deep maroon, red, or crimson inside; **spadix** sessile; cylindrical, sometimes clavate or weakly tapered, 7.2–8.5(9.5) cm long, ± uniform throughout; pistillate portion pale greenish, cylindrical, 1.8–2.4 cm long, 5.8–8 mm diam. at apex, 6–9 mm diam. at middle, 5–6 mm wide at base; staminate portion 4.8–8.9 cm long; fertile staminate portion white, cylindrical, clavate or weakly tapered, 6–11 mm diam. at base, 8–9 mm diam. at middle, 7 mm diam. ca. 1 cm from apex, as broad as or sometimes broader than the pistillate portion, if detectable, narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, white, 6 mm diam.; pistils 1–2.2 mm long, 0.6–1.4 mm diam.; ovary 5–8(10)-locular, 0.4–1 mm long, 0.8–1 mm diam., with sub-basal placentation; ovules 1(2) per locule, sometimes contained within transparent, gelatinous ovule sac, 0.2–0.5 mm long, equal in length to or longer than funicle; funicle 0.2 mm long, style 0.7 mm diam., similar to style type B; style apex with depressions surrounding stylar canal exits; stigma brush-like, discoid, 0.5(1.5) mm diam., 0.2–0.6 mm high, covering entire style apex; the androecium truncate, margins irregularly 4–5-sided, 1.3 mm long, 0.3–1.4 mm diam. at apex; thecae oblong, sometimes oblong-elliptical; pollen spheroidal to ellipsoidal or elongate, less than 0.2 mm long, 0.1 mm diam.; sterile staminate flowers 3–6-sided or irregularly 4-sided, 0.9–3.9 mm long, 0.4–1.3 mm wide. INFRUCTESCENCE pendent; seeds 1(2) per locule. JUVENILE leaves and spathes tinged red.

Flowering in *Philodendron bakeri* occurs from the early dry season, December through April, with post-anthesis collections from January through May.

Immature fruiting collections were made in May and June.

Philodendron bakeri is known along the Atlantic slope of Costa Rica from 100 to 900 m elevation in *Premontane wet forest* and *Tropical wet forest* life zones and also occurs in Central Panama at 900 to 1420 m in *Tropical wet forest* and *Premontane rain forest* life zones. It is expected to be found in intervening areas.

Philodendron bakeri is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. The species is characterized by its scandent habit, slender stems (frequently pendulous on flowering portions), reddish, deciduous cataphylls, subterete petioles (one-fourth to one-third as long as the blades), more or less oblong blades, and by the solitary inflorescence with the spathe green, suffused with red or maroon outside, and heavily suffused with red within, especially at the base. Also characteristic are the bright orange fruits.

Philodendron bakeri is most similar to *P. immixtum*, also a vine with more or less elongate blades. That species differs in having thicker internodes drying with broad fissures and an often loose, flaking epidermis, and thinner blades that dry greenish or greenish brown and are more typically subcordate at the base. In contrast, *P. bakeri* has minutely fissured stems that lack a loose, flaking epidermis and blades that dry typically reddish brown, moderately coriaceous, and are merely rounded to obtuse at the base.

Though both species have spathe tubes that are reddish on the inner surface, *P. immixtum* differs in that the tube is not reddish on the outside.

Both *P. bakeri* and *P. immixtum* are members of *P.* sect. *Calostigma* subsect. *Glossophyllum*, with one ovule per locule, but locules of *P. immixtum* differ in being longer, with the transparent envelope enclosing the ovules being about twice as long as the ovules, whereas those of *P. bakeri* have the ovule(s) embedded in a gelatinous matrix completely filling the envelope.

Philodendron bakeri may also be confused with precociously flowering shoots of *P. sagittifolium*. Both species have petioles that may be tinged purplish violet on both ends. *Philodendron sagittifolium* differs in having pistils with 7–8 locules with 2–4 ovules per locule in a transparent envelope (vs. 1 ovule per locule in a gelatinous matrix).

Croat 44312 from La Selva, Costa Rica, differs in drying dark gray-brown above, dark brown below, and in lacking secretory ducts. It is perhaps a juvenile of some other species.

The species is named in honor of Richard Baker, an aroid specialist previously at the Field Museum, who made the first collection in 1974.

Additional specimens examined. COSTA RICA. **Alajuela**: Cariblanco–Laguna Hule, ca. 2 km W of Costa Rica Highway 9, 10°17′N, 84°13′W, *Baker et al. 227* (F, MO); Monteverde Biological Reserve, Río Peñas Blancas, 900 m, 10°19′N, 84°44′W, *Haber & Bello 6932* (MO), *7907* (CR); Volcán Miravalles, W of Bijagua, near Río Zapote, ca. 600 m, 10°44′N, 85°05′W, *Burger et al. 11628* (F, MO); Cañas–Upala, 4 km NNE of Bijagua, on slopes leading into Río Zapote, ca. 400 m, *Croat 36263* (MO); Upala, 2 km NE of Colonia Libertad along Río Caño Negro, 300 m, 10°50′N, 85°16′W, *Herrera 1958* (MO); San Ramón, 800 m, *Bello 1973* (CR); *Bello et al. 4537* (CR, INB); Reserva Forestal de San Ramón, 1000 m, 10°12′40″N, 84°36′20″W, *Herrera 6748* (CR, MO). **Guanacaste**: N side of Lake Arenal, 1 km NW of dam, 650 m, 10°30′N, 84°46′W, *Haber et al. 4915* (CR, MO); *4916* (MO). **Heredia**: ca. 7 km SW of Las Horquetas, ca. 400 m, 10°18′N, 84°01′W, *Grayum 5018* (MO); ca. 8 km SW of Las Horquetas, 450–550 m, 10°18′N, 84°02′W, *Grayum et al. 6543* (MO); Río Peje–Río Sardinalito, Volcán Barva, 700–750 m, 10°17′30″N, 84°04′30″W, *Grayum & Jermy 6784* (MO); La Zona Protectora, Río Peje–Río Guacimo, northern slopes of Volcán Barva, along trail from main road across Quebrada Cantarana to Río Guacimo, 250 m, *Grayum & Schatz 3219* (DUKE); La Selva Field Station, 100 m, *Hammel 7805* (DUKE, MO); 100–150 m, *Croat 44312* (MO); 6 km by road from Río Peje crossing, 5 km SSE of Magsasay, 10°21′N, 84°03–04′W, *Schatz & Grayum 667* (DUKE); Magsasay, 700 m, *I. Chacón 182* (MO). **Limón**: Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson et al. 6982* (LAM); Tortuguero National Park, 0 m, 10°34′N, 83°31′W, *Croat 61210* (MO); 2 km W of Río Toro Amarillo on road W from Guápiles, 275 m, 10°13′N, 83°50′W, *Thompson & Rawlins 1225* (CM). PANAMA. **Chiriquí**: Cerro Colorado, 19.7 mi. N of Río San Félix, 1420 m, 8°31′N, 81°46′W, *Croat 74997* (MO). **Coclé**: Penonomé, Llano Grande–Coclecito, 4.3 mi. N of Llano Grande, 410 m, 8°42′N, 80°26′W, *Croat 67456* (CM, L, MO, PMA); El Copé region, Alto Calvario, 5.2 mi. above El Copé, 930 m, *49159* (MO); above Alto Calvario, 1200–1300 m, *Sytsma & Andersson 4546* (MO); El Valle region, La Mesa, above El Valle de Antón, 860–900 m, *Croat 37419* (MO), *37508* (MO). **Panamá**: El Llano–Cartí Road, Km 19.1, 350 m, 9°19′N, 78°55′W, *de Nevers & Herrera 5875* (MO, PMA); El Llano–Cartí, Nusagandi, 325–350 m, *Croat 67395* (MO); Km 10, *33710* (MO); 0.5 mi. E of El Llano, *D'Arcy 5202* (MO).

Philodendron basii Matuda, Anales Inst. Biol. Univ. Nac. Méxic. 32: 153, Fig. 8. 1961. TYPE: Mexico. México: Barranca de Malinaltenango, NE (published as SE) of Zacualpan, 1200 m, 18°43′N, 99°36′W, *Matuda 37244* (holotype, MEXU). Figures 76, 81–84.

Almost always terrestrial, or trailing over rocks; stem green, stout, succulent, leaf scars conspicuous, 2–4 cm long, 4–5 cm wide; internodes 1–4 cm long, 2.5–7 cm diam., broader than long, drying olive-green, epidermis peeling, light brownish,

roots long, 5 mm diam., light reddish tan; cataphylls 20–28 cm long, weakly to sharply 2-ribbed, medium green with darker ribs and dark green speckles in lower one-half of cataphyll, drying tannish, persisting intact, eventually deciduous; **petioles** 22–70 cm long, 8–15 mm diam., terete, medium green, surface dark striate; **blades** ovate-cordate, drying moderately thin, weakly bicolorous, semiglossy, acute at apex, cordate at base, 16–56 cm long, 9–38 cm wide (1.5–1.8 times longer than wide), (0.7–0.9 times the petiole length), broadest at or above middle; upper surface medium green, weakly glossy, drying medium yellow-brown; lower surface slightly paler, semiglossy, drying yellow-green to yellow-brown; margins sinuate or weakly undulate; anterior lobe 35–48 cm long, 37.5–46 cm wide (2.5–8.5 times longer than posterior lobes); posterior lobes 4–19 cm long, 18–23 cm wide, directed inward, rounded to obtuse at apex; sinus spathulate, 10–13 cm deep; midrib weakly sunken to flat, heavily dark green striate, paler than surface above, convex, sparsely dark-lineate, paler than surface below; basal veins 3–6 per side, with 1 pair free to base, the third through fifth coalesced 3–3.5(4) cm; posterior rib naked for 1–2.5 cm; primary lateral veins 4–7 per side, departing midrib at a 40–60° angle, ± straight to the margins, sunken and paler than surface above, convex and paler than surface below; interprimary veins sunken and concolorous above, flat and darker than surface below; branches of primary lateral veins ± ruffled-sunken and concolorous above, raised and paler than surface below; minor veins predominately arising from the primary lateral veins, those arising from the midrib seem to disappear soon after leaving the midrib. INFLORESCENCES probably 1 per axil; peduncle 7–8 cm long, 7–8 mm diam., green; **spathe** 12.6–13.7 cm long (1.7–1.8 times longer than peduncle), apiculate at apex; spathe blade pale green or white, tinged red near base outside, 8 cm long, white tinged with red near base, pale-speckled inside; spathe tube ellipsoid, dark green outside, 6 cm long, 3 cm diam., maroon-red (B & K Red-Purple 10/3) inside; **spadix** sessile; tapered, 11.8–12 cm long, broadest at the base; pistillate portion cylindrical, 2.5–3.8 cm long, 1.5–1.9 cm diam. midway, slightly narrower on both ends; staminate portion 7.6–13 cm long; fertile staminate portion clavate, 9–15 mm diam. at base, 11–15 mm diam. at middle, 5–10 mm diam. ca. 1 cm from apex, broadest above the middle, narrower than the pistillate portion, broader than the sterile portion; sterile staminate portion narrower than the pistillate portion, 1–1.8 cm diam.; pistils 2.9–3.9(5.7) mm long, 1.4–2 mm diam.; ovary 4–6-locular, 2 mm long, 1.4 mm diam., with sub-basal placentation; ovules 4–6 per locule, 2–3-seriate, contained within transparent ovule sac, 0.3 mm long, equal in length to funicle, style similar to style type D; style apex rounded, with style boss and with depressions surrounding stylar canal exits; style boss narrow but pronounced; stigma slightly discoid to hemispheroid, 1.6–2.2 mm diam., 0.6–1.4 mm high, covering almost entire style apex; the androecium 4–6-sided; thecae oblong, 0.3 mm wide; sterile staminate flowers 4–6-sided, 1.7 mm long, 0.9–1.6 mm wide. JUVENILE leaves ± sagittate at base.

Flowering in *Philodendron basii* is recorded during the early wet season with post-anthesis collections made during September and in January, although too few collections overall have been seen.

Philodendron basii is endemic to Mexico, ranging from western Jalisco, south and east to the states of Colima, México, and Guerrero, at 350 to 1200 m elevation in "Bosque Pino-Encino" and "Selva Baja Caducifolia." Matuda (1962) reported it from as low as 200 m elevation.

Philodendron basii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Pachycaulia.* The species is characterized by its very stout, green, succulent stems, which usually trail over rocks; weakly two-ribbed cataphylls, which remain intact and are usually soon deciduous; long-petiolate, moderately thin, ovate cordate blades with a sinuate margin; and by the green spathes with the tube reddish purple within.

Although *Philodendron basii* is not easily confused with any other species, it is ecologically very similar to *P. warszewiczii,* which also has thick, succulent, bare stems and occurs in very dry habitats. The latter is distinguished by its deeply dissected leaf blades. Matuda compared *P. basii* with *P. smithii,* to which it bears only a superficial resemblance. That species differs in having more slender internodes, which are usually longer than broad; more narrowly ovate blades; and (usually) two inflorescences per axil with longer peduncles.

Though no specimens have been seen from Colima State in Mexico, Matuda (1962) reported having seen this species there.

Additional specimens examined. MEXICO. **Guerrero**: km 337–338 beyond Acahuizotla on highway to Acapulco. 3000 ft., *Moore 5100* (BH, CM); road to Xalpatlahuac between bridge over Río Omitlan and confluence of Río Papagayo with Río Omitlan, 850 m, *Croat 45766* (MO). **Jalisco**: Highway 200, 10–13 km SE of El Tuito, valley of Río las Juntas, 250–330 m, *McVaugh 25396* (MICH); ca. 6 mi. S of Tuito, 350 m, *Croat 45442* (COL, MEXU, MO, US).

Philodendron breedlovei Croat, sp. nov. TYPE: Mexico. Chiapas: Mun. La Trinitaria, Monte Bello National Park, E of Lago Tzikaw, 13 May 1973, *Breedlove 35181* (holotype, DS; isotype, MEXU). Figures 79, 80, 85.

Planta hemiepiphytica; internodia usque plus quam, 7 cm, ca. 1.5 cm diam.; cataphylla decidua; petiolus subteres, 34 cm longus, 7 mm diam.; lamina anguste ovato-cordata, usque 37 cm longa, 20 cm lata, in sicco flavi-brunnea; inflorescentia 1; pedunculus 6 cm longus, 6 mm diam.; spatha 10.5 cm longa; lamina spathae viridalba vel alba; tubo spathae extus virenti, intus rubro; pistilla 5–6-locularia; loculi 20-ovulati.

Hemiepiphytic; internodes to 7 cm or more long, ca. 1.5 cm diam., usually longer than broad, drying light brown, semiglossy, weakly and irregularly ribbed; cataphylls deciduous; **petioles** 34 cm long (slightly longer than blades), 7 mm diam., subterete; **blades** narrowly ovate-cordate, acuminate and slightly inequilateral at apex, sagittate at base, 37 cm long, 20 cm wide (1.8 times longer than wide; about equal in length to petiole), semiglossy, upper surface drying dark olive-green, lower surface drying yellowish brown; anterior lobe 31.5 cm long, 21 cm wide (4 times longer than posterior lobes); posterior lobes 7.5 cm long, 8.7 cm wide, narrowly rounded, directed toward base; sinus ± V-shaped, 5–6 cm deep; midrib drying narrowly raised and darker below; basal veins 3–4 per side, with 0 free to base, 1 pair coalesced for 2.8 cm; posterior rib to 3 cm long, not naked; primary lateral veins 5–6 per side, arising initially at an acute angle then forming a gradual arch to margin, departing midrib at a 55° angle toward apex, 60–70° angle midway, to 80° angle near the base, weakly arcuate to the margins, drying weakly raised and paler below; minor veins arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 6 cm long, 6 mm diam.; **spathe** 10.5 cm long (1.75 times longer than peduncle), slightly constricted midway, densely speckled-lineate, especially on the tube, red within, darker red on the tube within, weakly acuminate at apex, convolute to half its length at base; spathe blade greenish white to white, paler along the margins outside; spathe tube medium green outside, 5 cm long; **spadix** sessile; 6.5–8 cm long, broadest above the middle; pistillate portion 2.9 cm long, 1.7–1.9 cm diam., broadest at the middle; staminate portion 7.2 cm long; fertile staminate portion to 2.2 cm diam. midway, usually broader than the pistillate portion; sterile staminate portion 1.7 cm diam.; pistils 3.3–3.8 mm long, 1.7–1.8 mm diam.; ovary 5–6-locular, with axile placentation; ovules 20 per locule, 0.3–0.4 mm long, equal in length or slightly longer than funicle; style similar to style type B, 1.3–1.5 mm diam.; style apex truncate, minutely warty, irregularly 3–5-sided; stigma 2.3–2.5 mm diam., depressed with 5–6 small stylar canals; sterile staminate flowers 2.7–3.1 mm long, 0.9–1.6 mm wide.

Flowering in *Philodendron breedlovei* is based on a single collection in post-anthesis condition made in May. Flowering is probably in the early wet season, which begins in May in Mexico.

Philodendron breedlovei is known only from the type locality in Mexico (Chiapas) in "Bosque Pino-Encino" or "Bosque Caducifolio," at 1300 m elevation. Since its type locality is very near Guatemala, it is expected to be found there as well.

Philodendron breedlovei is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* The species is characterized by its long internodes; subterete petioles about equaling the blades; narrowly ovate-cordate, yellow-brown drying blades; solitary, short-pedunculate spathes with the outer surface white on the blade and reddish on the tube; and especially by its ovaries, which have parietal placentation and about 20 ovules per locule.

Philodendron breedlovei is most easily confused with *P. sousae* Croat, which has similarly shaped blades with weakly coalesced basal veins that often dry a similar yellow-brown color. That species differs in having only 1–3 basal ovules per locule and persistent stigmas bearing a conspicuous rim. The old stigmas of *P. breedlovei* instead are truncate and smooth with up to six more or less equally spaced stylar canals in a ring around the center.

Philodendron brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 140. 1937. TYPE: Costa Rica. Alajuela: La Palma de San Ramón, 1050–1100 m, *Brenes 5110* (holotype, F). Figures 36, 86–89.

Hemiepiphytic, sometimes terrestrial; stem gray-green, to 2 m long, glaucous; sap watery, spicy-scented; internodes weakly glossy, becoming matte, 2.5 cm long, 2.5–5 cm diam., about as long as broad, medium to dark green, weakly glossy to semiglossy, drying gray, epidermis brown, crisp; cataphylls to 24 cm long, sharply 1-ribbed to sharply 2-ribbed, sharply and broadly sulcate, pale green to greenish brown to reddish or weakly tinged red near base, densely short dark lineate, drying tannish brown, promptly deciduous, obtuse at apex, margins clear to pale; **petioles** 20–53 cm long, 0.6–1.7 cm diam., subterete, somewhat spongy, yellowish green, very broadly convex to weakly flattened to obtusely flattened with obtuse medial rib

adaxially, rounded to convex abaxially, with adaxial margins rounded, surface sparsely short, dark green or reddish lineate, sometimes with green to reddish ring around apex; **blades** narrowly ovate, subcoriaceous, short- to long-acuminate at apex, ± sagittate at base, 28–79 cm long, 8–38 cm wide, (1.6)1.8–2(2.4) times longer than wide, 1.1–1.4 times longer than petioles, upper surface medium to dark green, semiglossy to glossy, lower surface pale green to bluish green, matte to glaucous; anterior lobe 30–52 cm long, 20–30 cm wide (4.3–5.5 times longer than posterior lobes); posterior lobes 5.5–12 cm long, 8.8–13 cm wide, rounded, directed toward base; sinus narrowly V-shaped; midrib very broadly convex to flat, whitish to pale green to pale reddish green, sometimes sparsely short red-lineate, at least near base above, narrowly convex to convex, pale green to reddish, matte, sometimes dark red-lineate below; basal veins 5–6 per side, 2 free to base, the third and fourth sometimes coalesced to 3.5 cm; posterior rib not naked; primary lateral veins (5–6)8–12(18) per side, departing midrib at a 60–95° angle, sunken above, convex and paler than surface below; minor veins visible, etched-sunken and paler above, slightly raised and slightly darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1–2 per axil; peduncle 4.5–10.5 cm long, 0.5–1 cm diam., convex adaxially, rounded to angular abaxially, medium green, semiglossy; **spathe** thin, 9.5–18 cm long (1.7–2.1 times longer than peduncle), constricted ± at the middle, pale yellowish green throughout, spathe blade cream inside; spathe tube 4–6 cm long, semiglossy outside, deep magenta with resin canals inside; **spadix** sessile, ± tapered, 11.5–17.3 cm long, broadest at the base; pistillate portion pale yellow, cylindrical, 2.8–8 cm long, 0.8–1.4 cm diam., tapered toward base; staminate portion 8.6–10.8 cm long, only slightly broader than pistillate portion; fertile staminate portion cream, generally tapered, 9–14 mm diam. at base, 1.1–1.2 cm diam. at middle, 4–6 mm diam. ca. 1 cm from apex, broadest at base, usually narrower than the pistillate portion; sterile staminate portion 1–1.5 cm diam.; pistils 3.1–4.7 mm long, 1.7–2.8 mm diam.; ovary 5–8-locular, 1.8 mm long, 1.7 mm diam., with sub-basal placentation; ovules 6–12 per locule, arranged in 2 series of 6 ovules, contained within gelatinous matrix (no true envelope), 0.4 mm long, ± equal in length to funicle, style 1 mm diam., similar to style type B; style apex flat to weakly rounded; stigma subdiscoid, 1.5–2.1 mm diam., 0.3–1.7 mm high, inserted on center of style apex, shallowly depressed medially; the androecium truncate, 4–6-sided; thecae oblong to ovate, 1.3 mm wide, contiguous; pollen cream, elongate to subspheroidal, 0.1–0.2 mm long, to 0.1 mm diam. INFRUCTESCENCE with berries yellow maturing to orange; seeds 2 per locule, very pale yellow, 1.4–1.7 mm long, 0.7 mm diam. JUVENILE plants creeping, appressed-climbing; internodes 8–15 mm long, 2–2.5 cm wide; petioles 7–8 mm diam, D-shaped, flattened adaxially, weakly striate; blades narrowly ovate, 19–23.3 cm long, 9–12 mm wide; basal veins 1–2; posterior rib not naked; primary lateral veins 5–10 per side.

Flowering in *Philodendron brenesii* may be aseasonal. Flowering collections have been made in July and August, and many post-anthesis collections have been made between March and November. Fruiting collections have been made mostly during what is the dry season and early wet season in Costa Rica, December through May. Mature fruiting collections have been made in December, January, February, and May.

Philodendron brenesii ranges from Costa Rica to central Panama, at 800 to 2200 m elevation in *Premontane rain forest* and *Tropical Lower Montane rain forest* life zones.

Philodendron brenesii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata.* The species is distinguished by its mid-elevation habitat, bright green internodes about as long as broad, sharply two-ribbed, promptly deciduous cataphylls, and narrowly ovate blades with a narrow V-shaped sinus, more or less free basal veins, and a more or less bluish green lower surface.

Philodendron brenesii is most easily confused with *P. crassispathum* Croat & Grayum, which has similar venation but more broadly ovate blades and a nearly ellipsoid spathe with very thickened walls (usually more than 1 cm thick) and no sign of a constriction between the blade and tube portions. The peduncle on the latter is sometimes so short that it appears to be lacking. In contrast, the spathe of *P. brenesii* is of normal thickness and shape (e.g., the spathe is divided into a tube and blade portion). *Philodendron straminicaule* can sometimes be confused with the more narrow-leaved forms of *P. brenesii,* but that species differs in having a hippocrepiform, rather than a narrowly V-shaped, sinus.

The leaf blades of *Philodendron brenesii* closely resemble those of *P. validinervium* Engl. from coastal Ecuador between Nanegal and Gualea. That species differs in having proportionately longer and narrower posterior lobes, more closely spaced and prominently raised primary lateral veins, a long-pedunculate spathe (1.2 times longer than the pe-

duncle vs. 1.6–3.1 times longer), and a 4-locular ovary with about 4 ovules per locule (vs. a 5–7-locular ovary with up to 12 ovules per locule).

Philodendron brenesii is one of the most commonly cultivated species throughout the Meseta Central in Costa Rica. A specimen collected in Coclé Province of Panama (*Croat 67578*) is somewhat disjunct from the nearest populations in Chiriquí Province, but perhaps belongs here as well. The material has juvenile blades more broadly ovate than in other populations of the species. It also lacks the bluish green coloration on the lower blade surface and has the dried midrib dark rather than pale. The adult blades of the Coclé collections are remarkably similar to those of the Chiriquí collections, and the other differences may be due to the fact that these plants occur near the lower part of the elevational range. A number of differences in the pistil argue that this collection may represent a different species. Pistil differences in the Coclé collection include, among other things, the presence of a style funnel and a style dome (lacking in the Chiriquí populations). The Coclé collection also has eight locules per ovary and two seeds per locule, perhaps another important difference.

A Costa Rican collection (*Herrera et al. 8789*) from Tarrazú in San José Province is unusual in having smaller leaves with indistinct primary lateral veins and petioles drying minutely wrinkled. The dried blade color, minor venation, and dried stem characters otherwise match *P. brenesii*. While this might represent a new species, more information is needed. *Herrera et al. 8789* also is similar in stature and blade shape with *P. knappiae* from Chiriquí Province in Panama. The collection differs from *P. knappiae* in its pale gray-green drying (vs. dark brown) lower blade surface, lack of secretory ducts between the minor veins, and a deeply sunken style into the apex of the pistil on drying (vs. a style held above the apex of the pistil on drying).

Additional specimens examined. COSTA RICA. **Alajuela**: San Ramón–Balsa, ca. 5.7 km N of Quebrada Volio, 1100–1150 m, 10°08′N, 84°29′W, *Stevens 14124* (CR, F, MO, NY, US); Cerro el Chayote–Zarcero, *Poveda 1187* (CR, F, MO); 8.9 mi. NW of San Ramón, 1100 m, 10°10′30N, 84°30′W, *Croat 68084* (B, CM, DUKE, F, K, M, MEXU, MO, NY, US); 1.3 mi. N of Angeles Norte, 1200 m, *Croat 46879* (MO); ca. 11 mi. NW of Zarcero, 900 m, *Croat 43521* (CR, MO); 1.5 km past Zarcero, 1800 m, *Hoover 1350* (CR, MO); Volcán Poás–Volcán Barba, 7 mi. N of Carrizal, 1850 m, *Croat 35491* (F, MO). **Cartago**: ca. 7.3 km NE of Pacayas, 5200 ft., *Wilbur et al. 16086* (MO); road to Moravia, ca. 20 km E of Río Pacuare, 1150 m, 9°50′N, 83°24′W, *Thompson & Rawlins 1230* (CM); Cerro de la Muerte, between summit & Empalme, 1800 m, *Croat 35415* (CR, L, MEXU, MO); La Cangreja, 10 km S of El Tejar, 1850 m, *Williams et al. 24191* (F, NY); Río Grande de Orosi, 15 km S of Tapantí, E slope above río, 1500 m, *Burger & Liesner 6713* (F); Río Naranjo, 3.5 km E of Cachí, 1360 m, *Lent 1431* (F); Tapantí Hydroelectric Reserve, along Río Grande de Orosi, 4.5 km beyond small bridge, 1500–1700 m, *Croat 36111* (MO); ca. 1 km S of jct. of Quebrada Salto & Río Grande de Orosi, 1500–1800 m, 9°43′N, 83°47′W, *Croat & Grayum 68226A* (MO); 1200 m, *Lent 990* (F). **Guanacaste**: Guachipelín–El Volcán de la Vieja, *Brenes 15565* (F, NY); SW slopes of Volcán Rincón de la Vieja and Volcán Santa María, trail from Hacienda Guachipelín, 1400 m, 10°48′N, 85°21′W, *Burger & Pohl 7771* (CR, F, MO, PMA); Fila del Volcán Cacao, 1400–1520 m, *Chacón & Chacón 2302* (MO); 1 km N of Las Nubes village, 8 km NW of Monteverde, 1200 m, 10°22′N, 84°51′W, *Haber & Zuchowski 9519* (CR, INB, MO, MV); Río Colorado, 820 m, 10°46′30″N, 85°20′35″W, *Rivera 660* (CR, MO). **Heredia**: 2 km S of Vara Blanco, 1900 m, *Wilbur et al. 15711* (DUKE); NW slopes of Volcán Barba, Río San Rafael, *Lent 1299* (CR, F, US); Volcán Poás–Vara Blanca, 1.5 km past divide in road, 1930 m, 10°12′N, 84°10′W, *Hoover 1347A* (MO, W); La Zona Protectora, Río Peje–Río Guácimo, N slopes Volcán Barba, 800 m, *Grayum & Schatz 3232* (DUKE); Río San Rafael, Atlantic slope of Volcán Barva, 1500 m, 10°13′N, 84°05′W, *Grayum et al. 7750* (MO). **Limón**: Moravia, 1300 m, *Williams 16171* (EAP); Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut, between Río Dapari and Río Lari, 1350 m, 9°23′50″N, 83°05′10″W, *Herrera 5384* (INB, MO); Talamanca, Río Lori, 1700 m, *Fernandez 816* (CR, INB). **Puntarenas**: Monteverde Cloud Forest Reserve, 1450–1650 m, 10°18′N, 84°47′W, *Burger & Baker 9767* (CR, F); 1700 m, 10°20′N, 84°50′W, *Haber & Bello 4115* (MO); 1700 m, *Haber 2413* (MO); 1550–1600 m, *Haber & Zuchowski 9827* (INB, MO); Zarcero region, Palmira, 5700 ft., *A. Smith 143* (F); Osa, vic. Boscosa, *Croat 78806* (CR, INB, MO). **San José**: vic. of Vara Blanca, 1880 m, *Croat 35519* (MO); Río Pará Blanca, Cerros de Zurquí, 1600–1800 m, 10°13′N, 84°01′W, *Burger et al. 10242* (F, MO); SW fork of Río Pará Blanco, lower slopes of Cerro Zurquí, *Utley & Utley 1270* (F); La Palma–San Jerónimo, *Utley & Utley 532* (F); 2 km N of Highway 12, ca. 10 km W of Inter-American Highway, 2200 m, *Croat 43387* (CR, MO); along CA-2, Cerro de la Muerte, N of turn off for road 222, 2000 m, *Croat 32857* (MO); Patarrá, Cerro El Espino, 1600–1800 m, 9°53′N, 84°02′W, *Chacón & Herrera 1586* (CR, MO); Aserrí, Cerros de Escazú, 1950–2100 m, *Morales 1305* (CR, INB); Rincón de la Vieja, *Boucler 233* (CR); Tarrazú, *Herrera et al. 8789* (MO). PANAMA. **Chiriquí**: Callejón Seco, Volcán de Chiriquí, 1700 m, *Woodson & Schery 510* (F, GH, MO); 4 km past divide in road to Alto Quiel from Boquete, 1600 m, 8°49′N, 82°28′W, *Hoover 1337* (MO); Gualaca-Chiriquí Grande, 5.9 mi. beyond Los Planes de Hornito, 1225 m, 8°45′N, 82°14′W, *Croat 67793* (AAU, CM, COL, CR, F, G, K, L, MEXU, MO, OOM, QCA, SAR, TEX, US); 5.5 mi. NW of Los Planes de Hornito, 1320 m, 8°40′N, 82°14′W, *Croat 74914* (MO); Cerro Colorado, ca. 13 mi. N of Río San Félix bridge, 800–1200 m, *Croat 33507* (MO); 24 mi. N of Río San Félix, 1430–1500 m, *Croat 48487* (MO); above San Félix, *33184* (MO); Los Planes de Hornito beyond Gualaca, 1400–1900 m, *Croat 48879* (MO, SAR, US); Boquete region, W of Río Caldera, ca. 2 km NW of Bajo Mono, 1700 m, 8°49′N, 82°28′W, *Grayum et al. 6448* (MO); 8.3 mi. W of Chame, 1300 m, 8°35′N, 81°50′W, *Croat 69090* (AAU, CR, MO, NY, PMA, VDB); near Continental Divide, 1500 m, *Antonio 1497* (MO, NY); Cerro

Hornito, S slope approached from Los Planes de Hornito, 1640 m, 8°41′N, 82°11′W, *Croat 67937* (CAS, MO); Cerro Horqueta, 1650 m, *Croat 27000* (CM, MO). **Coclé**: Alto Calvario along summit of Continental Divide 5.5 mi. N of El Copé, 3.5 mi. N of Escuela Barrigón, 850 m, 8°39′N, 80°36′W, *Croat 67578* (CM, CR, K, MO, NY, PMA, US); 1.5 mi. N of El Copé, ca. 900 m, *Croat 44577* (MO).

Philodendron brevispathum Schott, Bonplandia 7: 29. 1859. TYPE: Panama. Canal Zone: Chagres River, *Fendler 431* (holotype, MO; isotype, K). Figures 90, 91.

Philodendron arcuatum K. Krause, in Engl. & K. Krause, Pflanzenr. IV. 23Db (Heft 60): 72. 1913. TYPE: Bolivia. Pando: Río Acre, Cobija (on Brazilian border, SW of Rio Branco), 11°02′S, 68°44′W, *Ule 8819* (holotype, B).

Philodendron holmquistii G. S. Bunting, Acta Bot. Venez. 10: 297. 1975. *Philodendron brevispathum* subsp. *holmquistii* (G. S. Bunting) G. S. Bunting, Phytologia 64: 466. 1988. TYPE: Venezuela. Amazonas: Pueblo Viejo, open zone between the Río Pacimoni and the forest, 100 m, 1°50′N, 66°30′W, *Steyermark & Bunting 102495* (holotype, VEN; isotype, MY).

Terrestrial or hemiepiphytic; stem scandent, coarsely scabrous, densely covered with trichome-like, often branched scales; internodes elongate, 7.5–14(23) cm long, 8–15 mm diam., longer than broad, epidermis reddish brown, loosening and flaking, without fissures; roots drying tan to dark brown, few per node; cataphylls 6–9 cm long, soft, unribbed, green, drying dark reddish brown, eventually deciduous; **petioles** 10–43 cm long, 3–7 mm diam., subterete to bluntly C-shaped, somewhat spongy; **blades** ovate to ovate-triangular, concolorous, semiglossy, thin, acuminate at apex, cordate at base, 16–36 cm long, 11–26 cm wide (1.4–2 times longer than wide), (0.8–1.6 times longer than petiole), broadest at or above middle, upper surface semiglossy, lower surface semiglossy; anterior lobe 12–30 cm long, 10.8–24 cm wide (1.3–2.4 times longer than posterior lobes); posterior lobes somewhat triangular to narrowly triangular to rounded, or rounded to with hastate or flaring lobes, 5–15 cm long, 4.9–11.5 cm wide, subacute; sinus narrow or sometimes V-shaped, 9–11 cm deep; midrib sunken above, convex to raised, drying slightly paler below; basal veins 3–4 per side, with 1 free to base, coalesced 4–10 mm, or with 2–3 veins colaesced to 3 or 4 cm; posterior rib not naked or obscurely and briefly naked to 0.5 cm long; primary lateral veins (3)4–5 per side, departing midrib at a 55–70° angle, gradually ascending to the margins, weakly sunken above, convex and drying slightly darker below; interprimary veins almost as conspicuous as primary lateral veins; minor veins arising from both the midrib and primary lateral veins; tertiary veins visible and darker than surface below. INFLORESCENCES erect, 1 per axil; peduncle 1–7 cm long, 2.5–5 mm diam., subterete; **spathe** 6–10.5 cm long (1.4–4.6(9) times longer than peduncle); spathe blade green outside, red inside; spathe tube green to greenish white outside, 4–4.5 cm long, 2–2.5 cm diam., green to white inside; **spadix** sessile; 7–9.5 cm long, whitish to yellowish; pistillate portion 2–3 cm long, 3.5 cm diam. throughout; staminate portion 5–7 cm long; fertile staminate portion 5–10 mm diam.; sterile staminate portion 5–6 mm diam.; ovary ca. 6-locular, with axile placentation; ovules 6–14 per locule, 0.3–0.4 mm long, longer than funicle; funicle 0.2 mm long, adnate to lower part of partition, style similar to style type B; stylar canals emerging at base of pronounced apical depressions; style apex drying dark brown with a pale undulate margin and a central solitary stigmatic pad; the androecium truncate, prismatic, margins distinctly scalloped, irregularly 4–5-sided, 0.9 mm long; thecae oblong, 0.4 mm wide, nearly contiguous. INFRUCTESCENCE with peduncle 4 cm long, spathe 5–6 cm long; spadix, 3.5–4 cm long, 2.5 cm wide; berries pale yellow, 6 mm long, 3 mm diam.; seeds 4–6 per berry, oblong to weakly ovoid, 1.4 mm long, 0.4–0.5 mm diam.

Flowering in *Philodendron brevispathum* is apparently aseasonal, perhaps owing to its habitat along and near streams. Flowering collections have been made in February through April, July, August, and November. Immature fruiting collections were also made throughout most of the year, January through April, July, September, and November.

Though long known only from the Caribbean coast of Panama, *Philodendron brevispathum* is now known to be a locally rare but more widespread species with special ecological requirements. It ranges from Nicaragua to Panama at 0–280 m with disjunct populations in South America, there ranging from Venezuela to Brazil (Amazonas), Colombia (Vichada, Meta), Ecuador (Napo), Peru (Loreto), and Bolivia, at elevations of 60 to 230 m.

Philodendron brevispathum is a member of *P.* sect. *Philodendron* subsect. *Solenosterigma*. It grows as a low hemiepiphyte or in drier areas as a terrestrial herb, usually along streams, on river banks, or in swamps. *Maguire 36157* is unusual in being reported as a vine growing to 13 m in trees. The species is recognized by its scandent habit, its thin ovate to ovate-triangular leaf blades with rounded to hastate posterior lobes and a generally narrow (sometimes V-shaped) sinus, and especially by the stems that are densely covered with trichome-like, often branched scales and dry with a

flaky brown periderm. While the posterior leaf lobes are commonly somewhat triangular (and may even be narrowly triangular and subacute at apex), they may be nearly round on the same collection (*Davidse & Gonzalez 12973*).

Bunting (1988) distinguished the South American material as *P. brevispathum* subsp. *holmquistii*, characterized by having 7–14 ovules per locule (vs. 14–18 for the typical material in Central America) and pistils with the apex convex with 3–4 stigmatic pads. Yet my observations indicate that Central American material also has 6–14 ovules per locule.

This species is closest to *P. muricatum* Willd. ex Schott (an older name) and may not be separable from it. The latter species is distinguished by having densely verrucose-warty petioles and usually smaller blades with more rounded lobes. However, some collections with verrucose petioles such as *Steyermark et al. 115076* and *Liesner 9056* from Delta Amacuro, Venezuela, and *Krukoff 7250* from southern Amazonas State, Brazil (the type of *P. amplectans* A. C. Sm., a synonym of *P. muricatum*), have narrow, more or less triangular blades like those of *P. brevispathum*. On the other hand, not all specimens of *P. brevispathum* have similar lobes. Central American material commonly has more rounded or elongate lobes that are turned somewhat inward, but some sheets (e.g., *Burger & Antonio 11236*) have blades identical to those of South American plants. In addition, some South American collections (*Croat 58586, Davidse 4294*) have the posterior lobes noticeably rounded and scarcely longer than broad. Despite this variation, the verrucose petiole character is adequate to separate *P. brevispathum* from *P. muricatum*.

Philodendron brevispathum has also been confused with *P. jacquinii*, but that species has merely puberulent stems (with trichomes simple and unbranched), thinner, more broadly ovate leaves (often also puberulent on the petiole and lower midrib), a conspicuously bulging spathe tube, and more elongate styles.

Additional specimens examined. COSTA RICA. **Heredia**: Puerto Viejo–Guápiles, along Río Puerto Viejo, 7 km N of Buenos Aires, 10°23′30″N, 83°48′30″W, *Croat 68401* (K, MO); La Selva Field Station, *Grayum 2300* (DUKE, MO); *Grayum 2642* (DUKE, F, MO), 100 m, *Hammel & Trainer 10810* (DUKE); Río Frío de Sarapiquí, between Río Sucio and railroad tracks, SW of Finca Zona Ocho, 110 m, 10°18′N, 83°52′30″W, *Grayum & Hammel 5568* (MO). **Limón**: Río Bananito–Cahuita, near Punta Vargas ca. 4 km S of Cahuita, 0–10 m, *Burger et al. 10493* (F, MO); 16 airline km SW of Barra del Colorado, 10–120 m, 10°39′N, 83°40′40″W, *Davidse & Herrera 31254* (MO); Refugio Barra del Colorado, area between Río Chirripocito and Río Sardina, 12 m, 10°38′N, 83°45′W, *Grayum et al. 9742* (AAU, CR, MO); Finca Tapezco–La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8842* (MO); 40 m, 10°30′N, 83°47′W, *8970* (RSA, MO); Gandoca (slightly to N of trail from Mata de Limón), 0–5 m, 9°36′N, 82°36′30″W, *Grayum et al. 8024* (CR, K, M, MO); Cerro Coronel, 10–40 m, 10°40′N, 83°40′W, *Stevens et al. 24670* (CR, MO); Parque Tortuguero National Park, Tortuguero, 2 m, *Robles 1410* (CR, MO); 4 m, 10°32′N, 83°30′W, *Robles 1877* (CR, F, MO); near Boca de las Lagunas de Tortuguero, 0–30 m, 10°34′N, 83°32′W, *Burger & Antonio 11236* (F, MO, U). NICARAGUA. **Matagalpa**: Ranchería, 11 km al NE de Muy Muy, 280 m, 12°46′N, 85°31′W, *Moreno 24433* (MO). **Río San Juan**: Quebrada Santa Crucita, 50 m, 11°02′N, 84°25′W, *Moreno 23445* (MO); Sábalo, 1 km N of Río San Juan, 100 m, 11°02′N, 84°27′W, *26111* (MO); Boca de Sábalos, cerca de "La Toboba," 70–90 m, 11°03–04′N, 84°28–29′W, *Robleto 1833* (MO, US). **Rivas**: Isla de Ometepe, La Argentina, 300–800 m, 11°27′N, 85°32′W, *Moreno 22112* (CM, MO). **Zelaya**: La Barra de Punta Gorda, 0–2 m, 11°30′N, 83°47′W, *Moreno & Sandino 13298* (MO); Caño Monte Cristo, "La Grupera," 10 m, 11°33′N, 87°48′W, *Moreno & Sandino 14739* (MO); Puerto Cabezas–Río Wawa, Ibo Tingní, drainage of Caño Sung Sung, 10 m, 14°9–11′N, 83°29–31′W, *Stevens 10636* (ENCB, MO); Santa Marta, 5 m, 14°18′N, 83°37′W, *Stevens & Moreno 19623* (MO); SW of Bluefields, 10–40 m, 11°59′N, 83°46′W, *Stevens 19736* (CAS, L, MO, UWL). PANAMA. **Colón**: Miguel de la Borda, *Croat 10012* (MO, SCZ). **San Blas**: Playón Chico, road to Isisukun, 0–10 m, 9°20′N, 78°13′W, *Herrera 596* (MO).

Philodendron brewsterense Croat, sp. nov. TYPE: Panama. Comarca de San Blas: Cerro Brewster, 850 m, 9°18′N, 79°16′W, *de Nevers, Herrera, Hammel & Charnley 5545* (holotype, MO–3246994). Figure 92.

Planta epiphytica; caulis scandens; internodia 5–6.5 cm longa, 4–5 mm diam.; cataphylla leniter vel acute 2-costata, decidua; petiolus 9–11 cm longus, usque 4 mm diam., anguste et obtuse sulcatus; lamina ovata, leniter subcordata, 9.8–11 cm longa, 7–8 cm lata, in sicco flavibrunnea; nervis lateralibus 1 absentibus; inflorescentia 1; pedunculus 4.7 cm longus, 3.5 mm latus; spatha omnino in superficebus ambabus maronnina, 9–9.3 cm longa; pistilla 5-locularia; loculi 2-ovulati.

Epiphytic; stem scandent; leaf scars inconspicuous; internodes terete, 5–6.5 cm long, 4–5 mm diam., much longer than broad, drying yellowish brown, epidermis fissured narrowly; roots dark brown, drying moderately fuzzy, slender, 1 mm diam., very few per node; cataphylls weakly to sharply 2-ribbed, glossy, deciduous; **petioles** 9–11 cm long, to 4 mm diam., narrowly and obtusely sulcate adaxially, surface minutely wrinkled; sheath conspicuous, the tip free-ending (2–3 mm long); **blades** ovate, acuminate at apex (acumen inrolled, 1–2 mm long), weakly subcordate at base, 9.8–11 cm long, 7–8 cm wide (1–1.4 times longer than wide; about equal in length to petiole), broadest in lower one-third, margins revolute, drying reddish brown, upper surface medium green, drying grayish

green, semiglossy, lower surface weakly glossy, moderately paler, drying yellowish green; anterior lobe 9–10.5 cm long, 7–8 cm wide (5.9–7.1 times longer than posterior lobes), broadest in lower one-third; posterior lobes 2–2.4 cm long, 2.8 cm wide, rounded; sinus obtusely angular, 5 mm deep; posterior rib lacking; midrib concave above, moderately raised, drying paler than surface below; basal veins numerous on each side but none of them outstanding, primary lateral veins lacking or indistinguishable from minor veins; minor veins close, arising from the midrib only, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 4.7 cm long, 3.5 mm diam., dark brown; **spathe** erect, subcoriaceous, 9–9.3 cm long (2.1 times longer than peduncle), maroon throughout on both surfaces; spathe blade 6.9 cm long; spathe tube 4.5 cm long; **spadix** green throughout (probably juvenile), narrowly rounded at apex, 7.3 cm long, constricted below sterile staminate portion; pistillate portion drying grayish, slightly tapered toward the apex, 2.1–2.5 cm long in front, 1.2 cm long in back, 4.5–5 mm diam. at apex, 5–6.8 mm diam. at middle; staminate portion 4.5–6.1 cm long; fertile staminate portion white, gradually tapered towards apex, 6.5–6.8 mm diam.; pistils 1.1 mm long; ovary 5-locular, 0.9 mm diam., ovule sac ca. 0.5 mm long, with sub-basal placentation; ovules 2 per locule, contained within transparent ovule sac, ca. 0.2–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long (can be pulled free to base), style 0.7–0.9 mm diam., similar to style type D; style apex rounded; style boss broadly and gently rounded; stigma button-like, distinctly lobed, 1 mm diam., 0.3 mm high, covering entire style apex, inserted on style boss; the androecium truncate, prismatic, margins irregularly 4–6-sided, 0.9–1.1 mm long, 3–5 mm diam. at apex; thecae oblong to weakly ellipical, 0.4 mm wide, ± parallel to one another; sterile staminate flowers subrounded, 5–9 mm wide, grayish to pale orange.

Flowering in *Philodendron brewsterense* is based on a single flowering collection made in April in an area that is somewhat aseasonal.

Philodendron brewsterense is endemic to Panama, where it is known only from the type specimen collected on Cerro Brewster in Comarca de San Blas Province, at 850 m elevation in a *Premontane rain forest* life zone.

Philodendron brewsterense is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. The species is recognized by its scandent habit with internodes much longer than broad, drying yellowish brown and narrowly fissured; small (<8 cm diam., <11 cm long), coriaceous, ovate, yellowish brown blades lacking primary lateral veins; and solitary inflorescences with the outer surface surface maroon.

Philodendron brewsterense is apparently unrelated to any other species but is most similar to *P. crassispathum* and resembles juvenile plants of that species. The latter differs, however, in having juvenile leaves with an arcuate sinus and adult leaf blades usually more than 20 cm long and with four to six pairs of primary lateral veins.

Philodendron brunneicaule Croat & Grayum, sp. nov. TYPE: Panama. Coclé: Alto Calvario, 6 mi. N of El Copé, Atlantic slope along Continental Divide, along trail which heads off old lumber trail and leads down to Las Ricas, Limón, and San Juan, 710–800 m, 8°39′N, 80°36′W, 22 June 1988, *Croat 68713* (holotype, MO–3591332). Figures 93–97.

Planta hemiepiphytica; internodia 6–20 cm longa, 1–1.2 cm diam., rubrobrunnea; cataphylla 20–40 cm longa, incostata, decidua; petiolus teres vel C-formatus, leviter subcomplanatus adaxialiter 21–63 cm longus, 4–11 mm diam.; lamina ovata, cordata aut interdum sagittata basi, 25–62 cm longa, 16–52 cm lata; inflorescentia 1; pedunculus 4–20 cm longus, 8–9 mm diam.; spatha 11–21 cm longa; lamina spathae extus cremea, intus viridalba; tubo spathae extus viridi, intus cerasino; pistilla (5)6(7)-loculari; loculi (13)15–18-ovulati; baccae albae.

Hemiepiphytic; stem light reddish brown to rusty red, leaf scars conspicuous, 8 mm long, 12 mm wide; internodes sparsely short dark-lineate, sometimes weakly warty, semiglossy, 6–20 cm long, 1–1.2 cm diam., longer than broad, dark green to olive-green to brown, epidermis loosening and flaking, reddish brown; cataphylls soft, 20–40 cm long, unribbed, sometimes bluntly 1-ribbed, greenish white to white with margins pinkish, drying reddish, deciduous; **petioles** 21–63 cm long, 4–11 mm diam., erect-spreading to spreading, terete, to C-shaped, somewhat flattened adaxially, medium green, surface matte, sometimes striate and dark green- to red-lineate; geniculum 3 cm long, 2.5–3 cm diam., thinner and paler than petiole; **blades** ovate, subcoriaceous, bicolorous, acuminate at apex, cordate or sometimes sagittate at base, 25–62 cm long, 16–52 cm wide (0.6–1.75 times longer than wide), (0.7–1.6 times longer than petiole), upper surface dark green, glossy to semiglossy, lower surface glossy to semiglossy, paler; anterior lobe 23–65 cm long, 19–52 cm wide (0.88–1.5 times longer than wide); posterior lobes rounded to obtuse, 8–20 cm long, 9–26 cm wide; sinus spathulate to hippocrepiform; midrib flat to sunken, paler than

surface above, narrowly convex to round-raised, paler than surface, sometimes tinged maroon below; basal veins 5–9 per side, with 0–2 free to base, (2)3–4 coalesced 1.9–4.5 cm; posterior rib naked for 1–4.5 cm; primary lateral veins 4–6 per side, departing midrib at a 45–55° angle, conspicuously sunken above, narrowly convex and tinged maroon below; interprimary veins weakly raised and darker than surface below; minor veins arising from both the midrib and primary lateral veins; tertiary veins visible and sometimes darker than surface below. INFLORESCENCES erect, 1 per axil; peduncle 4–20 cm long, 8–9 mm diam., medium green, whitish at base, short dark green lineate; **spathe** glossy, 11–21 cm long (1.05–2.85 times longer than peduncle), constricted midway above the tube; spathe blade cream outside, greenish white (at anthesis) inside; spathe tube 6.5–9 cm long, green outside, cherry-red inside; **spadix** 9–17 cm long, broadest above the middle or ± uniform throughout; pistillate portion cylindrical to obovoid, 3.8–7 cm long, 7–13 mm diam. at apex, 8–14 mm diam. at middle, 10–14 mm wide at base; staminate portion 4.6–17.5 cm long; fertile staminate portion clavate, 9–16 mm diam. at base, 12–20 mm diam. at middle, 7–10 mm diam. ca. 1 cm from apex, broadest at middle, broader than the pistillate portion, narrower than the sterile portion; sterile staminate portion as broad as or narrower than the pistillate portion, 0.9–1.6 cm diam.; pistils 1.3–3.2 mm long, 1–1.8 mm diam.; ovary 5(6)7-locular, 0.9–2.1 mm long, 0.9 mm diam., with axile placentation; ovules (13)15–18 per locule, 2-series, 0.1–1.7 mm long, longer than or equal in length to funicle, style 1.2 mm diam., similar to style type B; style apex rounded; stigma subdiscoid, lobed, 1.5 mm diam., 0.3 mm high, covering not quite entire style apex; the androecium truncate, 3–6-sided, 2.2 mm long; thecae oblong, 0.2–0.5 mm wide; sterile staminate flowers blunt with one side scalloped, 1–2.2 mm long, 0.7–1.9 mm wide. INFRUCTESCENCE with berries white. JUVENILE plants with internodes to 10 cm long, 4–10 mm diam.; cataphylls reddish, persisting at upper nodes, sharply C-shaped in cross section.

Flowering in *Philodendron brunneicaule* probably occurs in the early rainy season, but a single (post-anthesis) collection was made in January. Most post-flowering collections have been made between April and July, with immature fruits collected in August and October.

Philodendron brunneicaule ranges from Costa Rica to Panama, Colombia (Valle), and Ecuador (Esmeraldas), at 50 to 1300 m elevation in *Tropical wet forest* and *Premontane rain forest.*

Philodendron brunneicaule is a member of *P.* sect. *Philodendron* subsect. *Platypodium.* The species is characterized by its appressed-climbing habit, long internodes with thin, flaking reddish brown epidermis (hence the name "brunneicaule," from "brunneus" meaning brown, and "caulis" meaning stem), white, unribbed, deciduous cataphylls, somewhat adaxially flattened and red-lineate petioles, ovate blades with reddish-brown-drying veins, large, solitary inflorescences borne at several of the uppermost internodes, and green spathes colored cherry-red inside on the tube.

Philodendron brunneicaule is probably related to *P. ernestii* Engl. from Amazonian Ecuador and Peru. That species shares long internodes with flaking brown epidermis and similar, solitary inflorescences. It differs, however, in having stems that are often warty and petioles that are undulate-winged vs. more nearly terete for *P. brunneicaule.* It is noteworthy, however, that a single collection from Amazonas Department, Peru (*Vásquez & Apanu 19051,* MO), appears to lack a petiolar wing. This may prove to be *P. brunneicaule,* but if so it would be the first collection from east of the Andes.

In Central America *Philodendron brunneicaule* is most easily confused with *P. copense.* See that species for the differences.

Additional specimens examined. COSTA RICA. **Alajuela**: San Ramón-Balsa, ca. 16.7 km N of bridge over Quebrada Volio and ca. 7.5 km N of Río Balsa, 700–800 m, 10°10–15′N, 84°30–35′W, *Stevens 13859* (CR, F, MO); 4.6 km N of bridge over Río Balsa, 900–1000 m, 10°12′N, 84°31′W, *Stevens 13735* (MO); 4–7 km N of Balsa, 750 m, 10°13′N, 84°32′W, *Liesner & Judziewicz 14667* (CR, MO); 18–19 km N of San Ramón, 950 m, 10°10′N, 84°28′W, *Hammel et al. 15234* (MO); Reserva Biológica Monteverde Río Peñas Blancas, 900 m, *Bello 369* (CR, INB, MO); Río Sarapiquí, crossing to Colonia Virgen del Socorro, 740 m, 10°5.5′N, 81°10.5′W, *Grayum & Hammel 5517* (MO); 830 m, 10°16′N, 84°11′W, *Croat 68302* (CM, G, M, MO, NY). **Heredia**: Puerto Viejo–Guápiles, 7 km N of Buenos Aires, <100 m, 10°23′30″N, 83°48′30″W, *Croat 68402* (MEXU, MO); La Selva Field Station, *Grayum 2790* (F, MO). ECUADOR. **Esmeraldas**: Quinindé, Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Santa Isabela, 400–600 m, 10°21′N, 79°44′W, *Pitman & Bass 1085* (MEXU, MO, NY, QCNE). PANAMA. **Bocas del Toro**: Fortuna Dam area, Fortuna Dam–Chiriquí Grande, 2.8 road mi. N of Divide, 850–950 m, 8°45′N, 82°15′W, *McPherson 9661* (MO); 1.2 mi. N of Divide, 5.3 mi. N of bridge over Fortuna Dam, 910 m, 8°44′N, 82°17′W, *Croat 60468* (AAU, CM, CR, MEXU, MO, PMA, US); gravel road near Continental Divide, 1170 m, 8°44′N, 81°17′W, *Croat 66655* (L, MO). **Chiriquí**: Gualaca–Fortuna Dam, 10.1 mi. NW of Los Planes de Hornito, 1300 m, 82°17′W, 8°45′N, *Croat 49836* (COL, K, MO, NY); 9.4 km above El Copé, 750–900 m, *Croat 44733* (MO). **Coclé**: El Copé, Alto

Calvario above El Copé, 4.5 mi. N of El Copé, 580–740 m, 8°38′N, 80°36′W, *Croat 67532* (AAU, MO, W); 930 m, *49183* (MO, US). **Panamá**: El Llano–Cartí road, 10 km from Inter-American Highway, near El Llano, 330 m, *Croat 33823* (MO); Km 14, 350–500 m, *Folsom et al. 1483* (MO); 10.1 mi. above highway, 325–350 m, *Croat 67365* (MO). **San Blas**: El Llano–Cartí Road, km 19, 350 m, 9°19′N, 78°55′W, *de Nevers et al. 5599* (B, K, MO, PMA); 1–2 mi. N of Nusagandi, 250–275 m, 9°20′N, 79°W, *Croat & Zhu 76581* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río San Luis, past Escuela Agrícola Alto de Piedra, at Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66909* (MO).

COLOMBIA. **Valle**: Bajo Calima region, Buenaventura–Málaga, Km 28, 50–150 m, 3°59′N, 77°03′W, *Bay 240* (CUVC, MO).

Philodendron chiriquense Croat, sp. nov. TYPE: Panama. Bocas del Toro: Cerro Colorado, 9.2 km W of Chame, along trail E of road leading down to stream, 1450–1480 m, 8°35′N, 81°50′W, 6 July 1988, *Croat 69068* (holotype, MO–3599857; isotypes, B, CAS, CM, COL, CR, F, GH, K, MEXU, PMA, US). Figures 98–100, 107.

Planta hemiepiphytica; internodia 1–4 cm longa, (1.5–2)3–4(6–10) cm diam.; cataphylla (20)55–70 cm longa, acute 2-costata, suffusa rubra, in sicco rubrobrunnea, persistentia semi-intacta; petiolus subteres vel D-formatus, 27–108 cm longus, in sicco 9–15 mm diam.; lamina triangulari-sagittata, cordata basi, 32.5–91 cm longa, 11–44 mm lata; inflorescentia 3; pedunculus 9 cm longus, 8–9 mm diam., albus suffusus ruber; spatha 14.2 cm longa, lamina spathae extus alba, intus albida, suffusa marronina usque ad dimidium; tubo spathae extus pallide viridi, intus marronino; pistilla 5-locularia; loculi circa 14-ovulati.

Hemiepiphytic; stem appressed-climbing to 4 m high or creeping, to 30 cm long; internodes short, very thick, semiglossy, 1–4 cm long, (1.5–2)3–4(6–10) cm diam., much broader than long, medium to pale green, coarse white-ribbed at upper edge, completely hidden by cataphyll fibers, drying brown; roots several per node, to 4 mm diam., light reddish brown to dark brown with flaky lighter brown epidermis, weakly glossy; cataphylls (20)55–70 cm long, sharply 2-ribbed, sharply sulcate with acute marginal ribs, green, heavily tinged with red toward base, sometimes red throughout, drying reddish brown, with two low ribs, persisting semi-intact at upper nodes, as pale fibers at base, eventually as dark brown to reddish brown fibers; **petioles** 27–108 cm long, 9–15 mm diam., subterete to obtusely D-shaped, firm and flexible, obtusely to weakly flattened adaxially, with adaxial margins sharp to bluntly rounded, dark green, base reddish, weakly glossy, surface faintly and densely white striate to coarsely pale striate, drying dark brown; **blades** triangular-sagittate, moderately coriaceous to subcoriaceous, short- to long-acuminate at apex (the acumen sometimes inrolled), cordate at base, 32.5–91 cm long, 11–44 cm wide (1.34–3.28 times longer than wide), (0.58–1.05 times longer than petiole), about equal in length to petiole, broadest at or near point of petiole attachment, upper surface dark green, with velvety sheen, drying gray-green to yellow-brown above, lower surface yellow-green, semiglossy, paler, drying reddish brown below; anterior lobe 39.5–68 cm long, 22–53 cm wide (1.2–1.8 times longer than posterior lobes); posterior lobes 6.2–29.6 cm long, 10.3–26.5 cm wide, directed inward, obtuse to rounded; sinus parabolic, hippocrepiform or spathulate; midrib narrowly rounded to almost flat to weakly sunken, drying gray-brown, paler than surface above, narrow-rounded to convex, concolorous or paler than surface, drying reddish brown below; basal veins (3–4)5–8 per side, with 0–1 free to base, (1)2–3 coalesced 0.9–7.5(11.5) cm, posterior rib naked 2–4 cm, sometimes not naked but with the rib sometimes running very near the margin; primary lateral veins 7–8 per side, departing midrib at a 60–70° angle, nearly straight to the margins, obtusely sunken, concolorous or paler than surface above, prominently convex to narrowly rounded, concolorus or paler than surface below; interprimary veins many, distinct; minor veins fine, moderately distinct; "cross-veins" visible on lower surface, sometimes weakly visible above. INFLORESCENCES ± erect, 3 per axil; peduncle 9 cm long, 8–9 mm diam., white tinged red, pale white striate toward apex, turned at 100° angle to spathe at anthesis; **spathe** 14.2 cm long (1.57 times longer than peduncle), weakly constricted above the tube; spathe blade white outside, whitish, suffused maroon to about midway inside; spathe tube globose, 6 cm long, pale green, tinged red on front outside, densely short, pale streaked throughout outside, maroon inside, **spadix** stipitate to 5 mm long; ovate, 11.6–12.5 cm long, broadest below the middle; pistillate portion greenish white, clavate, 2.7 cm long, 1.6 cm diam. at apex, 1.5 cm diam. at middle, 1.1 cm wide at base; staminate portion 10.9 cm long; fertile staminate portion weakly tapered, 1.8 cm diam. at base, 1.6 cm diam. at middle, 1 cm diam. ca. 1 cm from apex, broadest at base, broader than the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, 1.8 cm diam.; pistils 4.4 cm long, 1.8 mm diam.; ovary 5-locular, with axile placentation; ovules ca. 14 per locule, 2-seriate, contained within gelatinous matrix (no true envelope), 0.6 mm long, longer than funicle, style 2 mm diam., similar to style type B; style apex rounded; stigma subdiscoid, lobed, 1.5 mm diam., 0.3 mm high, drying lobed, covering center of style apex; the androecium truncate, margins 4–6-sided; thecae oblong, 0.2 mm

wide; sterile staminate flowers blunt, 4 mm long, 1.6 mm wide. JUVENILE blades with lower surface dark maroon.

Flowering in *Philodendron chiriquense* is known only during July. While this is, in general, the early wet season in Panama, the region around Fortuna where the species is common is somewhat less seasonal than other areas of Panama.

Philodendron chiriquense is endemic to Panama, known from Bocas del Toro, Chiriquí, and Coclé Provinces in *Tropical Lower Montane rain forest* and *Premontane rain forest* life zones at 500 to 1630 m elevation. It is frequent in the cloud forests near the Continental Divide in the Fortuna Dam area.

Philodendron chiriquense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* The species is distinguished by its short, very thick internodes; sharply two-ribbed, red-tinged cataphylls, which persist as semi-intact, dark brown fibers; obtusely flattened to D-shaped, densely pale-striate petioles; huge, triangular-sagittate blades; and up to three inflorescences per axil with the spathe tube pale green outside and maroon within.

Philodendron chiriquense is similar to *P. copense,* which also has persistent reddish brown cataphyll fibers and reddish-brown-drying, more or less triangular blades, but that species differs in having petioles drying reddish brown, smooth and matte, with peeling periderm (usually blackened, minutely fissured and semiglossy in *P. chiriquense*), primary lateral leaf veins drying reddish brown and darker than the surface (pale and lighter than the surface in this species), and minor veins and "cross-veins" both distinct (minor not distinct and "cross-veins" scarcely or not at all visible in *P. chiriquense*).

The only collection from Coclé, *Croat 44566,* may represent another species. This collection differs from Chiriquí material in having the primary lateral veins scarcely paler than the surface and more prominent "cross-veins."

Additional specimens examined. PANAMA. **Bocas del Toro**: Cerro Colorado, 8.6 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69133* (CM, MO); 7 mi. W of Chame, 1500 m, 8°35′N, 81°50′W, *69215* (MO, NY). **Chiriquí**: Cerro Colorado, 28 mi. above San Félix, 1200–1500 m, *Croat 33266* (MO); 20.5 mi. N of Río San Félix, 8.3 mi. W of Chame, 1630 m, 8°32′N, 81°46′W, *Croat 75047* (MO, PMA); 6.6 mi. W of Chame, 1475–1485 m, *Croat 75011* (CM, MO, PMA); Fortuna Dam area, Gualaca–Chiriquí Grande, 1 km S of Continental Divide, 1075 m, 8°45′N, 82°18′W, *Croat 66865* (MO); Los Planes de Hornito, 1400 m, *Croat 48761* (CAS, L, MEXU, MO, NY, PMA); 7.9 mi. NW of Los Planes de Hornito, 1300 m, 8°44′N, 82°16′W, *Croat 49905* (K, MO, US); 8.3 mi. NW of Los Planes de Hornito, 1260 m, 8°44′N, 82°16′W, *Croat 49940* (MO); 10 mi. NW of Los Planes de Hornito, 1260 m, 82°17′W, 8°45′N, *Croat 50101* (MO); Fortuna–Chiriquí Grande, 1170 m, 8°44′N, 81°17W, *Croat 66666* (AAU, CAS, CM, COL, F, KYO, L, MEXU, MO, NY, PMA, QCA, RSA, SAR, TEX, US); 8°44′N, 82°17′W, *Croat & Zhu 76345* (MO); Fortuna Lake area, 3.4 km N of Quebrada Chorro, 1.6 mi. N of center of bridge over lake, 1205 m, 8°43′N, 82°14′W, *Croat 74956* (MO). **Coclé**: El Copé region, near Continental Divide, ca. 1.5 mi. N of El Copé, 900 m, *Croat 44566* (MO); Alto Calvario along summit of Continental Divide 5.5 mi. N of El Copé, 850 m, 8°39′N, 80°36′W, *Croat 67573* (MO, NY); ca. 6 mi. N of El Copé, 770 m, 8°38′N, 80°35′W, *Croat & Zhu 76780* (MO, PMA). **Veraguas**: Santa Fe region, ca. 15 km past Escuela Agrícola Alto Piedra above Santa Fe, Río Caloveborita, Atlantic watershed, 500 m, *Sytsma & Andersson 4772* (MO).

Philodendron chirripoense Croat & Grayum, sp. nov. TYPE: Costa Rica. San José: Canaán–Chirimol, above Río Chirripó del Pacífico, remnant forest along river and on steep slopes above river, 9°27′N, 83°37′W, 30 Dec. 1969, *Burger & Liesner 7139* (holotype, F; isotype, CR). Figure 101.

Planta hemiepiphytica; caulis scandens; internodia 20 cm longa, minus quam 3 mm diam.; cataphylla decidua; petiolus teres, 7–7.4 cm longus, 1 mm diam., obtuse complanatus adaxialiter; lamina anguste ovata, subcordata basi, 11–11.6 cm longa, 5–5.5 cm lata; nervis basalibus liberis ad basim; inflorescentia 1; pedunculus 6 cm longus, 4 mm diam.; spatha 7.4 cm longa, intus viridi vel rubella; pistilla (3)5–6(8)-locularia; loculi 8–12-ovulati.

Hemiepiphytic; stem scandent; internodes very long and slender, 20 cm long, less than 3 mm diam.; roots drying dark brown; cataphylls unknown, probably <10 cm long, lanceolate, deciduous; **petioles** 7–7.4 cm long, 1 mm diam., obtusely flattened abaxially; **blades** narrowly ovate, very long-acuminate at apex (the acumen 2.4–2.6 cm long), subcordate at base, 11–11.6 cm long, 5–5.5 cm wide (ca. 2 times longer than wide), (ca. 1.5 times longer than petiole), about equal in length to petiole, drying brown; posterior lobes rounded to obtuse, 2–3 mm long, 1.4–1.7 cm wide; sinus arcuate with blade decurrent on petiole, 2–3 mm deep; midrib drying with up to 5 ribs above; basal veins 2–3 per side, with all free to base, obscure; primary lateral veins 2 per side, departing midrib at a 40–45° angle, straight to the margins; minor veins arising from the midrib only. INFLORESCENCES nearly as long as leaves, probably 1 per axil; peduncle 6 cm long, 4 mm diam., 0.83 times the petiole length; **spathe** 7.4 cm long (1.2 times longer than peduncle), green to reddish within; **spadix** pinkish throughout (fide field notes, in part lost); pistils 2.2 mm long, 1.1–1.2 mm diam.; ovary (3)5–6(8)-locular, with axile placentation; ovules

8–12 per locule, mostly 1-seriate, 0.1–0.2 mm long, slightly longer than funicle; funicle ca. 0.1 mm long, adnate to lower part of partition, style similar to style type B; style apex domed; the androecium truncate, oblong, prismatic, margins irregularly 4–5-sided, 0.7–1 mm long; thecae oblong, 0.3 mm wide, ± parallel to one another; sterile staminate flowers irregularly 4–5-sided, 0.8–1.2 mm wide.

Flowering in *Philodendron chirripoense* is based on a single fertile collection made in December, which is the early dry season on the western slope of Costa Rica.

Philodendron chirripoense is known only from the type specimen from the Pacific slope of southern Costa Rica, in *Premontane wet forest* at 1000 m elevation.

Philodendron chirripoense is tentatively placed in *P.* sect. *Philodendron* subsect. *Canniphyllum.* The species is characterized by its scandent habit, very long and slender internodes (drying <3 mm diam.), slender petioles about as long as the small, narrowly ovate, subcordate blades, and especially by the inflorescence being longer than the petioles.

Philodendron chirripoense is not similar to any other species in either Central or South America, but it might be confused with *P. microstictum,* the only other species that has the inflorescence longer than the leaves. The latter has larger blades (more than 13 cm wide), which are often broader than long.

Philodendron clewellii Croat, sp. nov. TYPE: Panama. Darién: middle slopes of W side of Cerro Pirre, cloud forest, 850–1050 m, 29 June 1988, *Croat 68945* (holotype, MO–3589994; isotypes, F, K, PMA, US). Figure 102.

Planta epiphytica; internodia 12–18 cm longa, 3.5 cm diam., moderate nitida, fissurata; cataphylla mallia, acute 2-costata, decidua; petiolus subteres, obtuse complanatus adaxaliter, 24.5–53 cm longus, (2)7–14 mm diam.; lamina ovato-cordata, 30–59 cm longa, 20–45 cm lata, in sicco brunnea, nervis basalibus liberis (aut leniter coalatis); inflorescentia usque 6; pedunculus 3.5–16 cm longus, 3–6 mm diam.; spatha 4.5–7 cm longa; lamina spathae extus cremea, intus purpurascente cum margine albido; tubo spathae in superficiebus ambabus purpurascenti; pistilla 6(7)-locularia; loculi 2-ovulati.

Epiphytic; stem scandent, smooth, thick, moderately glossy; internodes moderately glossy, 12–18 cm long, 3.5 cm diam., longer than broad, medium green to dark gray-green, epidermis fissured weakly longitudinally; cataphylls 18–25 cm long, soft, sharply 2-ribbed, green, caducous; **petioles** 24.5–53 cm long, (2)7–14 mm diam., subterete, spongy, dark green, obtusely flattened adaxially, surface green or white streaked-lineate; **blades** broadly ovate-cordate, subcoriaceous, moderately bicolorous, acuminate at apex (the acumen 1–2 cm long), cordate at base, 30–59 cm long, 20–45 cm wide (1.25–1.83 times longer than wide), (0.95–1.65 times longer than petiole), upper surface dark green, drying brown, semiglossy, lower surface slightly paler, drying brown, sometimes red-brown or green-brown, semiglossy, paler; anterior lobe 26.7–42.2 cm long, 23–45 cm wide (2.36–3.95(5.28) times longer than posterior lobes); posterior lobes broadly rounded, often overlapping, 7–18 cm long, 12–21 cm wide, obtuse to rounded; sinus narrowly closed; midrib weakly raised to almost flat, purple-spotted, paler than surface above, convex, darker than surface below; basal veins 3–5 per side, all free to base (or weakly fused); posterior rib absent or to 1.5 cm long, not at all naked; primary lateral veins 4–7 per side, departing midrib at a 45–60° angle, straight to the margins, weakly sunken, concolorous above, raised below, secondary veins weakly visible; minor veins visible, sparse, discontinuous below, arising from both the midrib and primary lateral veins. INFLORESCENCES to 6 per axil; peduncle 3.5–16 cm long, 3–6 mm diam., drying 2–4 mm diam., green, heavily red-striped; **spathe** 4.5–7 cm long ((0.62)1.28–2.33 times longer than peduncle); spathe blade cream outside, purplish, with margins whitish inside; spathe tube purple outside, 2.5–3 cm long, 6–10 mm diam., purple inside; **spadix** sessile; clavate, 6 cm long; pistillate portion green, tapered toward the apex, 2.5 cm long, 6 mm diam. at apex, 7 mm diam. at middle, 8 mm wide at base; staminate portion 3.7 cm long; fertile staminate portion white, clavate, 7 mm diam. at base, 9 mm diam. at middle, 8 mm diam. ca. 1 cm from apex, broader than the pistillate or sterile portions; sterile staminate portion 7 mm diam.; pistils 1.6 mm long, 1.1 mm diam.; ovary 6(7)-locular, with sub-basal placentation; ovules 2 per locule, contained within translucent ovule sac, 0.2 mm long, equal in length to funicle, style similar to style type B; style apex concave; stigma discoid, unlobed, 0.6 mm diam., 0.1 mm high, covering interior faces of stylar funnel; the androecium truncate, 4–6-sided; thecae oblong to elliptical, 0.1–0.2 mm wide; sterile staminate flowers irregularly shaped, 2.1 mm long, 9 mm wide, the margins blunt. JUVENILE plants with internodes 5–6 cm long, 8 mm diam., dark green; petioles terete, sheathing to midway.

Flowering phenology in *Philodendron clewellii* is unclear because there are too few fertile collections. It has been collected in flower in December

and post-anthesis in June, giving a hint of a bimodal flowering. Though Cerro Pirre is not markedly seasonal, these two months in general would mark extremes, with December the general beginning of the dry season and June the beginning of the rainy season in Panama.

Philodendron clewellii is endemic to Panama, known only from the Serranía de Pirre, from 850 to 1560 m elevation in *Premontane wet forest.*

Philodendron clewellii is a member of *P.* sect. *Calostigma* subsect. *Oligocarpidium.* The species is distinguished by its thick, smooth stems; usually long internodes; sharply two-ribbed, deciduous cataphylls; subterete petioles; ovate-cordate, dark-brown-drying blades with free or weakly fused basal veins and narrow, closed sinus with often overlapping posterior lobes; and especially by its clusters of up to six small inflorescences per axil with long peduncles, and spathe purple on the outside of the tube and cream on the blade.

In fertile condition, *Philodendron clewellii* does not resemble any other described species, but the leaf blades are similar to those of *P. tysonii* Croat. That species differs in having no more than three, much larger inflorescences at anthesis (to 12 cm or more long). In addition, the leaves of *P. tysonii* usually dry darker. In the blade shape and lack of a naked posterior rib, it is similar to *P. grayumii* Croat. That species differs in having generally more reddish brown blades with a broader sinus and much stouter peduncles.

The species is named in honor of Andrew Clewell, who made several expeditions to Panama while working for Florida State University and who helped collect the type specimen.

Additional specimens examined. PANAMA. **Darién:** Cerro Pirre region, 1000–1400 m, *Gentry & Clewell 7028* (K, MO); Río Cana–Río Escucha Ruido, *Croat 37831* (MO); ca. 12 km N of Alto de Nique, 1520–1560 m, *Croat 37915* (F, MO); ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat 37946* (MO); middle slopes on W side, 800–1050 m, 7°56′N, 77°45′W, *Croat 68957* (MO).

Philodendron coloradense Croat, sp. nov. TYPE: Panama. Chiriquí: Cerro Colorado, along mining road 31.6 km beyond bridge over Río San Félix (10.6 km beyond the turnoff to Escopeta), 1690 m, ca. 8°30′N, 81°45′W, 15 July 1976, *Croat 37168* (holotype, MO–2395435). Figures 103–106.

Planta hemiepiphytica; internodia usque 10 cm longa, 3 cm diam., sparsim rimosa; cataphylla usque 20 cm longa, incostata, viridia, decidua; petiolus subteretes, 35–37 cm longus, 1.5 cm diam.; lamina ovato-cordata, 26–33 cm longa, 17.5–25 cm lata; inflorescentia 2–3; pedunculus 8 cm longus, ad angulum ca. 140° infra spatham flexus; spatha usque 10 cm longa, in tubo viridis, in lamina extus viridalba, intus viridis; pistilla 4–5-locularia; loculi 4–7-ovulatii.

Hemiepiphytic; appressed-climbing; internodes smooth, sparsely cracked but only weakly or not at all ribbed, somewhat flattened on one side (at least at the upper nodes), to 10 cm long, 3 cm diam., medium green, soon turning gray, drying light brown; cataphylls to 20 cm long, unribbed, green, deciduous; **petioles** 35–37 cm long, 1.5 cm diam., subterete, firm, drying reddish brown, obtusely flattened adaxially, surface drying finely and irregularly striate; sheathing at base, 4–5 cm long; **blades** ovate-cordate, subcoriaceous, semiglossy, weakly bicolorous, acuminate at apex, prominently cordate at base, 26–33 cm long, 17.5–25 cm wide, 1.3–1.6 times longer than broad, upper surface drying dark brown, lower surface drying dark yellow-brown; anterior lobe 20–23.5 cm long, margins convex; posterior lobes 9–12 cm long, directed somewhat upward at an angle to the midrib, drying directed toward the base; sinus obovate, 6.5–9 cm deep; midrib flat, pale green above, convex, paler than surface below; basal veins 4–6 per side, and with the first free to base, third and fourth veins coalesced 1.5–3.5 cm, pale green; posterior rib not at all naked or naked up to 2 cm, only weakly curved; primary lateral veins 4–5 per side, departing midrib at a 45–55° angle, weakly curved to the margins, pale green, weakly sunken above, weakly raised below, drying paler than surface, flattened, with acute margins below; interprimary veins only occasionally present; minor veins easily visible on both surfaces, arising from both the midrib and primary lateral veins, drying weak and paler than surface and usually alternating with blackened secretory ducts, surface minutely granular upon magnification. INFLORESCENCES 2–3 per axil; peduncle to 8 cm long, drying dark reddish brown, minutely striate, bent at ca. 140° angle beneath the spathe; **spathe** to 10 cm long, to 5 cm wide when flattened, drying dark reddish brown throughout within, spathe blade pale green outside, drying reddish brown with prominent resin canals extending from the blade well into the tube within; spathe tube green, finely striate outside; **spadix** bluntly pointed at apex, 9 cm long; pistillate portion 2.5–2.7 cm long in front, 1–1.1 cm long in back, 10 mm diam. at apex, 9 mm diam. at middle; staminate portion 8.2 cm long; fertile staminate portion 1 cm diam. at base, 1.2 cm diam. at middle, 9 mm diam. ca. 1 cm from apex, sterile staminate portion 9 mm diam.; pistils 2.5 mm long, 1.4 mm diam.; ovary 4–5-locular, with axile placentation; ovules 4–7 per

locule, 2-seriate, 0.2 mm long, contained within transparent matrix; funicle 0.1–0.2 mm long, adnate to lower part of partition, style similar to style type B; style apex flat; stigma discoid, covering most of style apex except for center, drying irregularly 5-lobed, 0.9–1.3 mm diam.; the androecium truncate, weakly oblong, probably prismatic, margins irregularly 4–5-sided, mostly 4-sided, 1.3–1.6 mm diam. at apex; sterile staminate flowers irregularly 4–6-sided, prismatic, 1.4 mm wide. INFRUCTESCENCE with seeds 5–7 per locule, 0.4–0.5 mm long.

Flowering in *Philodendron coloradense* is documented by a single collection made in July, but the plant has three inflorescences, probably all of which opened after the onset of the rainy season in May. The region where the collection was made, though at a high elevation, is on the western slope of the Continental Divide, usually much affected by the dry season.

Philodendron coloradense is endemic to Panama, known only from near the Continental Divide at Cerro Colorado in Chiriquí Province at 1600 m elevation.

Philodendron coloradense is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. It is characterized by having grayish internodes longer than broad; green, unribbed, deciduous cataphylls; obtusely flattened petioles; ovate-cordate reddish-brown-drying blades with a spathulate sinus and a weakly developed posterior rib that is barely or not at all naked; and paired, green inflorescences bent somewhat at the apex of the peduncle.

The species is perhaps closest to *P. grayumii*, which differs in having 7–8 (vs. 4–5) locules per ovary and 3–4 (vs. 5–7) ovules per locule. In addition, the lower leaf surface of *P. grayumii* dries glossy and is epunctate with dense secretory ducts at higher magnifications. In contrast, the blades of *P. coloradense* dry more or less matte on the lower surface and are minutely speckled with only sparse secretory ducts at higher magnification.

Additional specimen examined. PANAMA. **Chiriquí**: Cerro Colorado, along mining road 20.5 mi. N of bridge over Río San Félix, 8.3 mi. beyond Chame and turnoff to Escopeta, 1630 m, *Croat 75039* (MEXU, MO, PMA, US).

Philodendron copense Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, 6 mi. N of El Copé, Atlantic slope, along Continental Divide, along trail which heads off old lumber road and leads down to Las Ricas, Limón, and San Juan, 710–800 m, 8°39′N, 80°36′W, 22 June 1988, *Croat 68765* (holotype, MO–3584056–8; isotypes, AAU, B, CAS, CM, COL, CR, K, PMA, US). Figures 109–111, 113–115.

Planta hemiepiphytica; internodia 1.5–2.5 cm longa; 2–7 cm diam.; cataphylla 7–25 cm longa, plerumque 1-costata, in sicco flavibrunnea vel atribrunnea, persistentia semi-intacta; petiolus acute D-formatus, 53–109 cm longus, 8–20 mm diam., epidermide interdum dense brevi-lineata, in sicco atriflavibrunneus; lamina ovato-triangularis, cordata, 56–84.5 cm longa, 22–47 cm lata, in sicco rubrobrunnea; inflorescentia usque 6; pedunculus 7–7.5 cm longus, 7–15 mm diam.; spatha 13–18.5 cm longa, lamina spathae viridi; tubo spathae viridi, extus suffuso purpureoviolaceo, pallidius secus marginem, intus marronino; pistilla 3–5-locularia; loculi 20–22-ovulati; baccae albae.

Hemiepiphytic; stem appressed-climbing, scandent; leaf scars inconspicuous; internodes short, thick, 1.5–2.5 cm long, 2–7 cm diam., broader than long, drying yellow-brown, epidermis moderately glossy, finely and acutely ridged on younger stems, lighter and more matte on older stems; roots drying brown, 15–75 cm long, 1–5 mm diam., numerous per node, epidermis peeling; cataphylls drying chartaceous, 7–25 cm long, usually 1-ribbed, pale red to reddish brown, drying yellowish brown to dark brown, persisting semi-intact as fibers. LEAVES erect to erect-spreading; **petioles** 53–109 cm long, 8–20 mm diam., sharply D-shaped, with broad medial rib adaxially, surface sometimes densely short-lineate, drying smooth and matte to semiglossy, light reddish brown or dark yellow-brown, the epidermis smooth and often flaking; **blades** ovate-triangular, moderately bicolorous to concolorous, abruptly acuminate at apex (the acumen (1)1.7–2.5 cm long), cordate at base, 56–84.5 cm long, 22–47 cm wide (1.8–2.7 times longer than wide), (0.77–1.1 times longer than petiole), broadest below point of petiole attachment, margins broadly undulate, occasionally downturned, upper surface dark green, glossy to semiglossy, drying reddish brown, gray-green or olive-green, matte to weakly semiglossy, lower surface drying semiglossy, yellow-brown to reddish yellow-green; anterior lobe 32–64 cm long, 20–46 cm wide (2.6–3.3 times longer than posterior lobes), broadest at or near base, margins concave; posterior lobes 14.5–21.5 cm long, 22–47 cm wide, broadest at or near base, directed downward and inward to downward and outward, obtuse to semirounded; sinus spathulate to widely hippocrepiform; midrib weakly raised to flat above, thicker than broad, paler than surface, drying concolorous or darker than surface below; basal veins 6–10(15) per side, with 1 free to base, numbers 4–7 coalesced 6–9 cm, prominently raised below; posterior rib naked for 3.5–4 cm; primary lateral veins 11–16 per side, departing midrib at a 55–90° angle, straight to weakly arcuate, drying reddish brown, sunken and paler than surface

above, raised, drying slightly darker than surface below; interprimary veins as conspicuous as primary lateral veins; minor veins arising from both the midrib and primary lateral veins; lesser veins drying prominulous; "cross-veins" moderately conspicuous on both surfaces. INFLORESCENCES erect, to 6 per axil; peduncle 7–7.5 cm long, 7–15 mm diam., green, coarsely lineate; **spathe** coriaceous, 13–18.5 cm long (1.8–2.6 times longer than peduncle), ± constricted midway on the tube, acute at apex; spathe blade green, short pale-lineate toward base, striate near apex outside, 10.5 cm long (opening broadly oblong-ovate in face view); spathe tube oblong-ellipsoid, green, tinged purple-violet, paler along margin outside, 8.5–9 cm long, 3.5 cm diam., maroon, conspicuously short-lineate inside; **spadix** sessile; oblong, 12.5 cm long, constricted at base of fertile staminate portion and tapering at both ends; pistillate portion white, cylindrical to ellipsoid, 6.5–7.5 cm long, 2.2–2.5 cm diam. throughout; staminate portion creamy white, 9 cm long, 9 mm diam. throughout, broadest in lower one-third; fertile portion 9–11 mm diam.; sterile portion narrower than the pistillate portion, 9–15 mm diam.; pistils 1.9–2.3 mm long, 1.9–2.3 mm diam.; ovary 3–5-locular, drying irregularly angled, walls embedded with granular, crystal-like particles, with axile placentation; ovules 20–22 per locule, style similar to style type B; style apex broadly and shallowly concave; stigma button-like, 0.5–0.7 mm long; sterile staminate flowers 2–2.4 mm long, 1–1.5 mm wide. INFRUCTESCENCE with berries white; seeds 0.8–0.9 mm long, 0.3–0.4 mm diam.

Specimens of *Philodendron copense* hint at bimodal flowering. A single flowering collection in post-anthesis condition was made in June, immature fruits were collected in January, and mature fruits were collected in December. The mature fruits in December could be the result of a flowering in the early rainy season, but immature fruits in January probably were the result of flowering in the late rainy season or early dry season. More flowering specimens are needed for more conclusive statements on phenology.

Philodendron copense is endemic to Panama (but should be expected in eastern Costa Rica) and is known from Bocas del Toro and Coclé (El Copé) at 590 to 930 m elevation in *Premontane rain forest.*

Philodendron copense is a member of *P.* sect. *Philodendron* subsect. *Platypodium.* This species is characterized by its appressed climbing habit; short, thick internodes (2–7 cm diam.); usually one-ribbed cataphylls which persist semi-intact; D-shaped petioles with flaky, yellow to yellow-brown epidermis upon drying; large, ovate-triangular blades drying reddish brown with many conspicuous "cross-veins"; and up to six inflorescences per axil with the spathes green or reddish tinged outside and maroon within on the tube.

Philodendron copense is most easily confused with *P. brunneicaule,* with which it occurs. Though the latter species has blades that dry a similar color, it is distinguished by having long internodes; deciduous cataphylls; petioles that lack the yellow-brown, peeling epidermis; ovate blades that lack the minute "cross-veins" upon drying; and stouter inflorescences that are solitary in each axil.

Philodendron copense is also similar to *P. chiriquense,* another species with an ovate-triangular leaf that dries reddish brown. *Philodendron chiriquense* differs by having much shorter, thicker internodes, conspicuous reddish brown persistent fibers (rather than semi-intact), and dark brown to blackened striate petioles, which lack an exfoliating smooth epidermis.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Fortuna–Chiriquí Grande, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat 60159* (CM, DUKE, F, MO, OOM, QCA). **Coclé**: near Continental Divide, along lumber road, ca. 1.5 mi. N of El Copé, 900 m, *Croat 44563* (MO, RSA, U); *44593* (COL, MO); 5.2 mi. above El Copé, 930 m, *Croat 49156* (L, MO, SAR, US); 5.6 mi. N of El Copé, 800 m, 8°39′N, 80°36′W, *Croat 75064* (M, MEXU, MO, NY, SCZ); *75091* (MO); ca. 5.6 mi. N of El Copé, 800 m, *75091* (MO); 9.4 km above El Copé, 750–900 m, *44729* (B, CR, K, MO, PMA, TEX).

Philodendron correae Croat, sp. nov. TYPE: Panama. Chiriquí: Gualaca–Chiriquí Grande, vic. Lago Fortuna, along trail to meteorological station on Río Hornito departing from N side of highway, ca. 0.5 km S of Centro de Científicos, 8°45′N, 82°18′W, 24 July 1994, *Croat & Zhu 76395* (holotype, MO–4619416; isotypes, B, CAS, COL, CR, F, K, NY, PMA, US, VEN). Figures 116–119.

Planta hemiepiphytica aut raro terrestris; internodia obtuse complanata uno latere, usque 7 cm longa, 1.5 m diam.; cataphylla (8)13–16 cm longa, incostata, decidua; petiolus D-formatus, 7–16.5 cm longus, plus minusve spongiosus; lamina plus minusve oblonga, rotunda vel leniter subcordata basi, 21–46 cm longa, 5–12 cm lata; nervis lateralibus I 4 utroque, leniter visibilibus supra; inflorescentia 1; pedunculus 10.5–12 cm longus; spatha 15–18.4 cm longa, extus flavialba, intus leviter palidiori; interdum viridis basi, tubo intus suffuso obscure rubro; pistilla 5–6-locularia; loculi 1-ovulati.

Hemiepiphytic or rarely terrestrial; stem appressed-climbing or spreading; sap viscous, unscented; internodes obtusely flattened on one side,

moderately glossy, to 7 cm long, to 1.5 cm diam., usually much longer than broad, medium green to tannish, drying gray, epidermis becoming grayish brown and peeling; roots mostly 15–30 cm long, drying 2–3 mm diam.; cataphylls (8)13–16 cm long, unribbed, green, deciduous, turning mushy; **petioles** 7–16.5 cm long, (3)6–15 cm diam., D-shaped, obtusely flattened (drying usually sulcate) adaxially, ± spongy, narrowly rounded abaxially, with adaxial margins raised, surface with a conspicuous purple-black ring around apex; sheathing usually to near the apex, with margins erect and incurled, the tip free-ending; **blades** ± oblong, subcoriaceous, semiglossy, conspicuously to moderately bicolorous, abruptly long-acuminate or sometimes acute at apex (the acumen inrolled if present), rounded to weakly subcordate at base, 21–46 cm long, 5–12 cm wide (3–5 times wider than long), (ca. 2–4 times longer than petiole); upper surface semiglossy, dark green to medium green, drying dark brown to blackish brown, lower surface glossy and slightly to moderately paler; sinus 5–12 mm deep; midrib flat to broadly convex, paler than surface above, convex or thicker than broad and bluntly acute, darker than surface below; basal veins lacking; primary lateral veins weak, 4–6 per side when present but sometimes not apparent, departing midrib at a 60–70° angle, arcuate to the margins, slightly sunken, weakly visible above, convex, slightly darker than surface, weakly visible below; minor veins fine, moderately visible to distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 10.5–12 cm long, 5–6(14) mm diam., subterete; **spathe** coriaceous, 15–18.4 cm long (1.43–1.75 times longer than peduncle), weakly or not at all constricted, spathe blade yellow-white (B & K yellow-red 9/7.5–10 (at anthesis)) throughout, slightly paler inside; spathe tube sometimes green outside, 6.5–7.5 cm long, 1.6–2 cm diam., slightly paler and tinged dull red inside; **spadix** 8–19 cm long; stipitate 7–10 mm long; pistillate portion green to pale yellow, cylindrical, 7.9 cm long, 1.3–1.4 cm diam. throughout; staminate portion 4–8.4 cm long; fertile staminate portion tapered; pistils glossy, 3.3–3.8 mm long, 2.3–2.6 mm diam.; ovary 5–6-locular, with sub-basal placentation; ovules 1 per locule, style similar to style type C; style funnel shallow, sometimes deep subcylindric; style apex rounded, somewhat flat, with simple funnel; stigma ± discoid, covering interior faces of stylar funnel. INFRUCTESCENCE (post-anthesis) with seeds 1 per locule, 1.5–1.7 mm long, 7–8 mm diam.

Flowering in *Philodendron correae* has been recorded only during the early rainy season, June through September, but relatively few fertile collections have been seen overall.

Philodendron correae is endemic to western Panama in Chiriquí and Bocas del Toro Provinces at 780 to 1400 m in *Premontane rain forest* and *Tropical Lower Montane rain forest.*

Philodendron correae is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is distinguished by its internodes generally longer than broad; more or less oblong, dark brown- to black-drying blades with rounded to weakly cordulate bases; primary lateral veins only weakly visible; and solitary inflorescences with the spathe blade yellowish white on both inner and outer surfaces.

Philodendron correae is closest to *P. ligulatum,* which differs in having rather prominent primary lateral veins and by occurring at generally lower elevations (sea level to 900 m). *Folsom et al. 5471* is noteworthy in having blades that dry greener than is usual for the species. It also has a Type B style type; the only other specimen studied for ovules (*Croat 66748*) had a Type C style. The difference may have been due to the age of the flowers, but this situation warrants further investigation.

Philodendron correae is named in honor of Mireya D. Correa A., among the first scientists to collect in the Fortuna area, and the first to collect this species.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60436* (CAS, L, MO); 6.6 mi. N of middle of bridge over Fortuna Lake, 780 m, 8°45′N, 82°18′W, *Croat 66779* (MO); along gravel road near Continental Divide, 1170 m, 8°44′N, 82°17′W, *Croat 66653* (MO, PMA, US). **Chiriquí**: Cerro Colorado, above San Félix, along mining road 18–27 mi. N of Pan-American Highway, 1200–1500 m, *Croat 33151* (MO); 13–14.6 km N of Chame, 1390–1410 m, *Croat 37217* (MO); Fortuna Dam area, N of Gualaca, 11.8 mi. N of Los Planes de Hornito, 1400 m, *Croat 48676* (MO, US); Gualaca–Chiriquí Grande, at junction of road to IRHE headquarters, 1200 m, 8°45′N, 82°18′W, *Croat 66748* (CM, CR, HMNM, HUA, MO); 1.4 mi. W of Centro de Operaciones, trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67917* (AAU, MEXU, MO, NY); Los Planes de Hornito, 1000–1200 m, *Correa 2256* (PMA); ca. 10.7 mi. from Planes de Hornito, 4000 ft., *Antonio 5148* (MEXU, MO); along aquaduct to IRHE water source near dam, 1200–1300 m, 8°45′N, 82°18′W, *Croat 66626* (MO); 1400–1500 m, *Folsom et al. 5471* (MO).

Philodendron cotobrusense Croat & Grayum, sp. nov. TYPE: Costa Rica. Puntarenas: along road about halfway between Flor del Roble and Las Alturas de Coto Brus, 1250 m, 8°54′N, 82°51′W, 13 July 1985, *Grayum & Hammel 5689* (holotype, MO–3446320; isotypes, CR, K, US). Figure 120.

Planta hemiepiphytica; internodia 1–3 cm longa, 1.5–2 cm diam., cum epidermide argenteocana; cataphylla usque 14 cm longa, acute 2-costata, decidua; petiolus 32.5–35 cm longus; lamina profunde 3-lobata, 37–38 cm longa, 46–52 cm lata, venis confertis; nervis lateralibus I 18–19 utroque; inflorescentia usque 5; pedunculus 6–9 cm longus; spatha 6–14 cm longa, lamina spathae extus cremeoflava, intus eburnea; tubo spathae extus viridi, intus rubro-violacio; pistilla 6–7-locularia; loculi 3-ovulati.

Hemiepiphyte; stem appressed-climbing; internodes short, thick, 1–3 cm long, 1.5–2 cm diam., mostly longer than broad, epidermis silvery gray; cataphylls to 14 cm long, sharply 2-ribbed, yellow-green, tinged pinkish, deciduous; **petioles** 32.5–35 cm long, 4–9 mm diam., subterete, firm, obtusely flattened adaxially, surface matte; **blades** deeply 3-lobed, margins incised to within 1.5–2 cm of base, subcoriaceous, weakly bicolorous, long-acuminate at apex (the acumen probably downturned), ± cordate at base, 37–39 cm long, 46–52 cm wide (0.7–0.8 times longer than wide), (1–1.2 times longer than petiole), usually about equal to petiole, upper surface dark green, semiglossy, lower surface weakly glossy, somewhat paler; median lobes 30.5–32 cm long, 13–17 cm wide; lateral lobes 24–27 cm long, 9–12.6 cm wide (2.14–2.88 times longer than wide), directed ± upward, broadly confluent to 2.5 cm with medial lobes; midrib broadly convex, closely veined above, convex below; basal veins lacking; primary lateral veins 18–19 per side, departing midrib at a 50–65° angle, broadly curved to the margins, sunken above, convex below; interprimary veins almost as conspicuous as primary lateral veins; tertiary veins visible, slightly darker than surface; minor veins arising from both the midrib and primary lateral veins but mostly from midrib in upper half of blade. INFLORESCENCES to 5 per axil; peduncle 6–9 cm long, 3–4 mm diam., terete; **spathe** 6–14 cm long (1.8–3.5 times longer than peduncle); spathe blade creamy yellow outside, creamy white inside; spathe tube green outside, red-violet to purplish inside; **spadix** 9.5–12 cm long; pistillate portion yellow-green, 7–10 mm diam.; staminate portion 5–8 cm long; fertile staminate portion white, 8–12 mm diam.; ovary 6–7-locular, with sub-basal placentation; ovule sac 1 mm long; ovules 3 per locule, digitately arranged in series of 2–3, contained within transparent ovule sac, 0.2–0.3 mm long, slightly shorter than funicle; funicle ca. 0.3 mm long (can be pulled free to base), style similar to style type B; style apex flat; stigma subdiscoid, 1 mm diam., 0.2–0.3 mm high, covering entire style apex; the androecium truncate, ± oblong, prismatic, irregularly 4–6-sided, 0.7–1.1 mm long; thecae oblong, 0.3 mm wide, ± parallel to one another.

Flowering in *Philodendron cotobrusense* has been recorded only during the early rainy season in July.

Philodendron cotobrusense is known only from eastern Costa Rica in the Cordillera de Talamanca, at 1000 to 1250 m elevation in a *Premontane wet forest* transition to *rain forest* life zone.

Philodendron cotobrusense is a member of *P.* sect. *Tritomophyllum.* This species is characterized by its appressed-climbing habit; sharply two-ribbed, deciduous cataphylls; short, thick internodes with a silvery-gray epidermis; petioles about equaling the deeply three-lobed, closely veined blades (with more than 16 pairs of primary lateral veins); and especially by the inflorescences in clusters of up to five per leaf axil with the spathe tube green outside, red-violet within, and the blade creamy yellow on the outside and creamy white within.

Philodendron cotobrusense is most similar to *P. madronense* Croat. That species differs in having the medial segment even more closely veined (to 18 or more) and not at all confluent with the lateral lobes. In addition, it has solitary inflorescences.

Philodendron cotobrusense is also similar to *P. tripartitum,* but that species differs in usually having narrower, oblanceolate to oblanceolate-elliptic blades with more widely spaced primary lateral veins (usually 4–10, rarely to 12), and fewer inflorescences per axil (up to three) with longer peduncles. In addition, *P. cotobrusense* has 3 ovules per locule whereas *P. tripartitum* has 1.

Davidse 24202, tentatively placed in *P. tripartitum,* seems to be somewhat intermediate with *P. cotobrusense.* See the discussion of that species.

Additional specimen examined. COSTA RICA. **San José**: General Valley, between Canaán and Chimirol, Río Chirripó del Pacífico, 1000 m, 9°27′N, 83°37′W, *Burger & Liesner 7119* (F).

Philodendron cotonense Croat & Grayum, sp. nov. TYPE: Panama. Chiriquí: vic. of El Hato del Volcán, at Las Lagunas, 3 mi. from Nueva California, 1.7 mi. past new airstrip, 1380 m, 8°46′N, 82°40′W, 17 Sep. 1987, *Croat 67708* (holotype, MO–3584981; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, K, L, G, NY, OOM, PMA, QCA, RSA, SAR, TEX, U, US, VEN). Figures 108, 121–123.

Planta plerumque hemiepiphytica; internodia 1–3 cm longa, 2.5–3 cm diam.; cataphylla 18–31 cm longa, incostata vel acute 1-costata, decidua intacta; petiolus subteretes, 17.5–53.5 cm longus, 5–8 mm diam.; lamina anguste ovato-triangularis, 23–45 cm longa, 11.5–20.5 cm lata; inflorescentia 1–2; pedunculus (6.5)10–17.5 cm longus, spatha 11–17 cm longa; lamina spathae extus di-

lute viridi vel cremeoflava vel alba, intus pallide viridi vel eburnea vel alba; tubo spathae extus atriviridi vel viridi, intus marronino vel carmesino pallide rubroviolaceo aut atripurpureo; pistilla 5–6-locularia; loculi 4–5-ovulatii; baccae vivide aurantiacae.

Hemiepiphytic vine or sometimes terrestrial; stem appressed-climbing but with ends often divergent, fertile to at least 5 m; leaf scars conspicuous, 1–1.3 cm long, 1.2–1.3 cm wide; internodes terete, semiglossy, sometimes matte, drying irregularly ridged, 1–3 cm long, 2.5–3 cm diam., usually broader than long, green, soon becoming gray to silvery-gray, drying yellowish brown, epidermis sometimes flaking free; roots short, stubby, light-colored at tips; cataphylls 18–31 cm long, unribbed to sharply 1-ribbed, yellow-green to green, promptly deciduous intact; **petioles** 17.5–53.5 cm long (averaging 34.4 cm long), 5–8 mm diam., subterete, weakly spongy, dark green, obtusely flattened, especially toward the apex adaxially, with abaxial margins broadly rounded, surface pale greenish lineate, semiglossy; **blades** narrowly ovate-triangular, subcoriaceous, usually gradually acuminate at apex (the acumen 1–3.5 cm long), prominently lobed at base, 23–45 cm long (averaging 35 cm long), 11.5–20.5 cm wide (averaging 15 cm wide), (0.7–1.4 times as long as petiole), broadest near point of petiole attachment, moderately bicolorous to almost concolorous, upper surface drying dark brown to dark olive-green, semiglossy, lower surface weakly glossy, usually yellow-brown, sometimes yellow-green; anterior lobe 16–31 cm long, margins weakly convex to flat or concave; posterior lobes 6–16.5 cm long, 3–8 cm wide, broadest at or near the middle, sometimes narrower at point of petiole attachment; sinus parabolic to obovate or almost oblong, 5–7.5 cm deep; midrib flat to weakly sunken, concolorous to paler than surface above, convex, paler than surface, often tinged purple (with coloration continuing onto petiole apex) below; basal veins 3–4 per side, the first often free to base (sometimes all free to base), the second and third coalesced 1–2.5(4.5) cm; posterior rib usually not naked except sometimes for up to 5 mm at the base; primary lateral veins (3)4–5(6) per side, departing midrib at a 30–65° angle (70–90° angle near base), weakly curved to the margins, sometimes drying undulate, often prominently downturned at midrib, sometimes tinged purplish, scarcely to weakly sunken above, narrowly raised below; minor veins obscure to clearly visible, arising from both the midrib and primary lateral veins, close and almost indistinguishable from the secretory canals, secretory canals appearing as intermittent lines, usually more prominently downturned at the midrib and appearing to cross over the minor veins, drying blackened. INFLORESCENCES 1–2 (usually solitary, sometimes 2) per axil; peduncle (6.5)10–17.5 cm long, subterete, pale-striate; **spathe** 11–17 cm long (0.94–1.6 times longer than peduncle), somewhat constricted above the tube; spathe blade light green to cream-yellow to white outside, pale green to cream-white to white inside; spathe tube dark to medium green, sometimes pale striate-lineate outside, 3–5.5 cm long, 1.3–2 cm diam., maroon to crimson pale red-violet or dark purple inside; **spadix** sessile, (6.7)10.5–16.5 cm long; pistillate portion green, cylindrical to ovoid, 2 cm long, 4–7 mm diam.; staminate portion 4.2–7.1 cm long; fertile staminate portion to 5 mm diam. throughout; sterile staminate portion whitish to cream-white, to 5 mm diam.; pistils 0.9 mm long; ovary 5–6-locular, 0.6 mm diam., with sub-basal placentation; ovules 4 or 5 per locule, arranged digitately, <0.1 mm long, longer than funicle; funicle <0.1 mm long, style 0.9 mm long, 0.5 mm diam., similar to style type C; style apex flat, drying with 5–6 depressions alternating with ribs from a raised center; stigma hemispherical, inserted on stylar funnel; the androecium irregularly 3–6-sided; thecae ovate to cylindrical; sterile staminate flowers 0.8 mm long. INFRUCTESCENCE with berries bright orange; seeds drying pale yellow-brown, narrowly ellipsoid, 1.3–1.5 mm long, 0.6–0.7 mm diam., with weak striations, appendages absent. JUVENILE plants with petioles 4.7–7.7 cm long; blades lanceolate (acumen 6.5–10.5 cm long), 1.7–2.5 cm wide.

Flowering in *Philodendron cotonense* has been recorded in both Costa Rica and Panama during June, and post-anthesis or early fruiting collections have been made from July through December (except October). Mature fruits have been collected only in March. However, several post-anthesis collections have been made during March, indicating perhaps a bimodal flowering period. Too few data are available to be certain.

Philodendron cotonense is known only from eastern Costa Rica and western Panama in *Premontane wet forest* and *Premontane rain forest, Tropical Lower Montane wet forest,* and *Tropical Lower Montane rain forest* life zones, as well as the transition zone between these zones, at 1100 to 1950 m elevation.

Philodendron cotonense is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by having internodes usually longer than broad (except distally), subterete petioles, and more or less triangular blades averaging over twice as long as broad, with posterior

lobes typically much longer than broad and often directed somewhat outward. Also characteristic are the conspicuous secretory canals visible on the dried blade surface and the solitary long-pedunculate inflorescences in each leaf axil.

Philodendron cotonense is most easily confused with *P. wilburii* var. *longipedunculatum*, which differs in having longer and more slender internodes (3–8 cm long and 8–15(20) mm diam.); sharply 2-ribbed cataphylls; and more typically hastate leaves ranging from 1.03 to 1.4 (averaging 1.29) times longer than wide, with proportionately narrower lobes directed outward at a broader angle (averaging 91° vs. 121° for *P. cotonense*). *Philodendron wilburii* var. *longipedunculatum* also differs in having mostly two inflorescences per axil with proportionately much longer peduncles, averaging 1.35 times longer than the spathe (vs. rarely longer than the spathe in *P. cotonense*).

Philodendron cotonense might be confused with smaller plants of *P. alticola*, which also have secretory canals visible on the blades. The latter species differs in typically having much larger blades (minimum 44 cm × 21 cm) that dry greener and thicker; persistent cataphyll fibers; and a short-pedunculate inflorescence with the spathe usually not at all constricted.

Noteworthy is *Davidse et al. 28367*, which has a narrower sinus and the basal veins all free to the base with the uppermost primary lateral veins more or less obscure. Otherwise, it fits well into *P. cotonense*.

Additional specimens examined. COSTA RICA. **Puntarenas**: vic. of San Vito de Java, ca. 1 km S of San Vito, on road to Villa Neily, 1100 m, *Croat 66169* (CR, K, MO, NY, US); 4000 ft., *Croat 32905* (MO); Zona Protectora Las Tablas, San Vito Coto Brus–Sabalito, Finca Neblinas, 1300–1800 m, 8°53′20″N, 82°50′30″W, *Mora et al. 54* (CR, MO); Flor del Roble–Las Alturas de Coto Brus, ca. 1250 m, 8°54′N, 82°51′W, *Grayum & Hammel 5690* (MO); Cerro Pando, ridges above Río Cotón and Río Negro, 1000–1800 m, 8°55′N, 82°45′W, *Barringer & Gómez 1606* (CR, F); Laguna Zoncho, San Vito, Coto Brus, 1200 m, *Gómez-Laurito 10774* (F); Las Alturas, along Río Cotón, 1340 m, 8°56′30″N, 82°50′W, *Davidse 24093* (CR, MEXU, MO); Cordillera de Talamanca, area around Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 1500–1600 m, 9°02′N, 82°59′W, *Davidse et al. 28367* (MO); sitio Cotón–Mellizas, 1300–1450 m, ca. 8°54′N, 82°46′W, *Davidse et al. 25562* (CR, K, MO); N of Santa Elena on Fila Cotón, S of Agua Caliente, 1100 m, 8°57′N, 82°56′W, *Davidse et al. 28236* (COL, CR, MO); N of Alturas, 1400–1500 m, 8°57′N, 82°50′W, *Davidse 24166* (CR, MO, US); around Tres Colinas, 1800–1850 m, 9°07′N, 83°04′W, *Davidse et al. 25606* (CR, MO); Las Cruces Botanical Garden, Coto Brus, ca. 4 km SE of San Vito, 1150–1200 m, 8°47′30″N, 82°58′W, *Grayum et al. 8113* (CM, CR, L, MO, QCA); Río Coto Brus, near Cotón, 23 km N of La Unión, *Croat 26692* (MO); Río Cotón, vic. of first large concrete culvert before Finca Las Alturas at Cotón, ca. 1300 m, *Croat 44349* (MO); Río Piedras Blancas, Cerro Anguciana, Fila Costeña, Fila Cruces, 950–1150 m, 8°49′18″N, 83°11′15″W, *Grayum 10646* (CR, INB, MO, VEN). PANAMA. **Chiriquí**: Volcán–Río Sereno, 7 mi. N of Volcán, 8°50′N, 82°38′W, *Croat 66226* (CM, MO, PMA, US); 13.7 mi. W of Volcán, 1200 m, 8°51′N, 82°43′W, *Croat 66343* (MO); vic. of Boquete, Cerro Pate Macho, upper NE slopes and summit, 1900–2000 m, 8°46′N, 82°25′W, *Croat 66504* (CAS, L, MEXU, MO, PMA).

Philodendron crassispathum Croat & Grayum, sp. nov. TYPE: Panama. Chiriquí: Cerro Colorado, above San Félix along mining road, 18–27 mi. off Pan-American Hwy., above Chame (turnoff to Escopeta), 1200–1500 m, 8°35′N, 81°50′W, 12 Mar. 1976, *Croat 33150* (holotype, MO–2395067; isotypes, B, F, K, PMA, US). Figures 112, 124, 127, 128, 149.

Planta hemiepiphytica, interdum terrestris; internodia 1.5–8 cm longa, (1–1.8)2.5–3.5 cm diam.; cataphylla carnosa, 8.5–24 cm longa, persistentia semi-intacta, denique decidua; petiolus subteres, obtuse complanatus, 20–31(48) cm longus, 5–19 mm diam.; lamina ovato-cordata, 14–29 cm longa, 11–24 cm lata; inflorescentia 1; pedunculus 3.5–7 cm longus, 1–2.5 cm latus; spatha carnosa, haud constricta, (6.8)10–14 cm longa, lamina spathae extus rubra extus, rubra vel alba intus; tubo spathae extus viridi, interdum extus flavido aut aurantiacorubro, intus violaceopurpureo vel rubro; pistilla 6–7-locularia; loculi 7–10-ovulati; bacca virides, aurantiacentes vel albidae.

Hemiepiphytic, sometimes terrestrial; stem appressed-climbing or scandent, creeping, becoming matte and gray, smooth when fresh, sap watery, spicy-scented, leaf scars conspicuous, 9–20 mm long, 2–3.5 cm wide; internodes drying conspicuously wrinkled, epidermis weakly glossy, 1.5–8 cm long, (1–1.8)2.5–3.5 cm diam., usually broader than long, dark green, epidermis brownish and cracking; roots dark brown, smooth upon drying, elongate, 3–50 cm long, 1–3 mm diam., few per node; cataphylls fleshy, 8.5–24 cm long, sharply 2-ribbed, green to dark green, dark green short-lineate, drying yellowish brown to pale green, persisting semi-intact at upper nodes then eventually fibrous then deciduous. LEAVES erect-spreading to spreading; **petioles** 20–31(48) cm long, 5–19 mm diam., subterete, somewhat spongy, sometimes tinged brown near apex, obtusely flattened with obtuse medial rib adaxially, convexly rounded abaxially; **blades** broadly ovate-cordate, very coriaceous, acuminate at apex (the acumen inrolled, 2–5 mm long), cordate at base, 14–29 cm long, 11–24 cm wide (1–1.56 times longer than wide), broadest at or near the middle, margins hyaline, whitish or reddish, tightly curled under when dried, upper surface dark green, glossy, drying semiglossy to

matte, lower surface paler, drying greenish gray to yellowish green to brownish, drying semiglossy to matte; anterior lobe 10–25 cm long, 11–33 cm wide (1.6–2.5 times longer than than posterior lobes); posterior lobes 4.5–10 cm long, 5–16.5 cm wide, obtuse to rounded; sinus spathulate to hippocrepiform; midrib flat to very broadly convex, drying yellowish green, paler than surface above, weakly convexly raised, paler than surface below; basal veins 3–4(6) per side, with 0–1 free to base, most of the remainder coalesced 1–2.5(4.4) cm, flat above, weakly raised below; posterior rib not naked if present; primary lateral veins 4–6 per side, departing midrib at a 40–70° angle, ± straight to the margins, flat, paler than surface, drying obscure above, raised and paler below; interprimary veins obscure above, weakly visible below; minor veins etched above, visible and darker than surface below, arising from midrib only. INFLORESCENCES shorter than leaves, 1 per axil; peduncle 3.5–7 cm long, 1–2.5 cm diam. (dried), terete, drying brown; **spathe** fleshy, (6.8)10–14 cm long, 4.5–10 cm diam., not at all constricted, ± ellipsoid, bluntly acute to rounded at apex, the walls to 1 cm or more thick midway; spathe blade red outside, red to white inside; spathe tube green, sometimes yellowish to orange-red outside, violet-purple to red inside; **spadix** (6.5)9–14 cm long; pistillate portion grayish to golden-yellow, cylindrical to slightly ellipsoid, 1.5–7 cm long, 10–25 mm diam. throughout, with 13–15 flowers visible per spiral; staminate portion 5–9 cm long; fertile staminate portion white with orange-brown droplets, cylindrical, weakly constricted above sterile portion, tapered toward apex, 15–23 mm diam. throughout, broader than pistillate and sterile portions, 22–27 flowers per spiral; sterile staminate portion 17–24 mm diam.; pistils 4–4.5 mm long, 4–4.5 mm diam.; ovary 6–7-locular, with axile placentation; ovules 7–10 per locule, 0.6–1 mm long, 0.3 mm diam.; funicles with free portion ca. 1 mm long, the remainder loosely fused to the wall of the locule; style similar to style type D, button-like and concave on drying, 1.3–2 mm diam., the margins pale; androecium margins irregular, 0.6–1.3 mm long; sterile staminate flowers ± globose, 1.4–2.2 mm long. INFRUCTESCENCE erect; pistillate spadix 4.5–5 cm long, 4 cm diam.; berries green becoming orange to whitish; pericarp white; mesocarp yellowish white; seeds yellow-orange, 2.9–3.5 mm long, 0.7–1 mm diam.

Flowering in *Philodendron crassispathum* appears to occur during the dry season and early rainy season based on flowering collections made during February through April and in August. Post-anthesis collections have been made from January through October. Mature fruiting collections have been made only from January through March, indicating that they may take up to almost one year to develop.

Philodendron crassispathum ranges from central Costa Rica to western Panama, at 1100 to 2600 m elevation in *Premontane rain forest* and *Tropical Lower Montane rain forest* life zones.

Philodendron crassispathum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata*. The species is characterized by its high elevational habitat, fleshy, deciduous, sharply two-ribbed cataphylls, subterete, obtusely flattened, somewhat spongy petioles, coriaceous ovate-cordate blades with the minor veins etched above, and especially by the very fleshy more or less ellipsoid, green spathe with walls typically 1 cm or more thick, colored white within on the blade and red in the tube.

Philodendron crassispathum is most closely related to *P. brenesii*, which differs in having narrowly ovate blades with a narrow V-shaped sinus and mostly free basal veins, and a comparatively thin spathe clearly constricted above the tube portion. In contrast, *P. crassispathum* has blades with a typically spathulate to hippocrepiform sinus and a usually obvious posterior rib.

Additional specimens examined. COSTA RICA. **Alajuela**: Río San Pedro, Cerro Azahar, 15 km NW of San Ramón by air, 1400–1500 m, 10°9′30″N, 84°34–35′W, *Liesner et al. 15502* (CR, K, MEXU, MO, WIS); Monteverde Reserve, Cerro Chomogo, 1600–1690 m, *Dryer 1470* (CR, F). **Cartago**: Río Dos Amigos–Río Villegas, narrow ridge W of Río Grande de Orosi, 1650 m, 9°42′N, 83°47′W, *Grayum et al. 3762* (MO, PMA, US); 4.5 km past town of Río Macho, along road to Humo, 1633 m, 9°17′N, 83°45′W, *Hoover 1346* (CR, MO); Tapantí Reserve, Quebrada Salto–Río Grande de Orosi, ca. 1 km S of jct., 1500–1800 m, 9°43′N, 83°47′W, *Croat & Grayum 68226* (CR, MO), *Grayum et al. 6301* (MO); 1380 m, *Croat 79077* (CR, INB, MO); Tapantí Watershed Preserve, 20 mi. SW of Paraíso, *Croat 47045* (CM, MO), *47043* (MO, SCZ). **Heredia**: Río Las Vueltas–Río Nuevo, E slopes of Volcán Barba, 2000 m, 10°6′N, 84°03′W, *Burger & Baker 9500* (CR, F, ISC, MO, NY, PMA); 9 km SE of Virgen del Socorro, 9 km E of Isla Bonita, 1530 m, 10°14′N, 84°05′W, *Loiselle 228* (MO); Cerro Chompipe, N of San Rafael, 2000 m, *Lems s.n.* (F, NY, US); Cerro de las Caricias, N of San Isidro, 2000–2400 m, *Standley & Valerio 51910* (US); San Rafael–Río Las Vueltas, N slope of Cerro Chompipe, 2100–2200 m, 10°05′N, 84°04′W, *Stevens 13989* (MO); Volcán Barva, Cerro Chompipe, near Ermita Santa Cruz, *Lems s.n.* (F, US); Río Las Vueltas, 12 km NE of San Rafael, 2000 m, *Wilbur et al. 15986* (DUKE); Río Santo Domingo, ca. 3 km E of San Rafael de Vara Blanca, N slope of Volcán Barva, 2060–2100 m, 10°11′N, 84°07′W, *Grayum 7335* (MO). **Limón**: Cantón de Talamanca, Bratsi, Amubri, Alto Lari, Kivut, between Río Lari and Río Dapari, 1900 m, 9°22′45″N, 83°06′15″W, *Herrera 5504* (INB, MO); Cordillera de Tal-

amanca, Cerro Biricuacua, 2600 m, 9°23′55″N, 83°10′10″W, *Herrera 6219* (CR, INB, MO); 9°20′20″N, 83°13′33″W, *Bittner 1864* (INB, MO). **Puntarenas**: Monteverde Reserve, 1500 m, ca. 10°17′N, 84°48′W, *Croat 61195* (MO); Cerro Negro, 1500–1600 m, *Haber & Bello 2843* (MO); Brillante Trail to Veracruz, river valley along Continental Divide, 1600 m, 10°20′N, 84°50′W, *Haber et al. 4584* (MO). **San José**: S slopes of Cerro Zurquí, ca. 4–4.5 km N of San Isidro de San José, 1500–1800 m, *Utley & Utley 408* (DUKE); 4 km N of Cascajal, 7 km N of Las Nubes, on CR-216, 1500–1600 m, *Utley & Utley 5255* (MO). PANAMA. **Bocas del Toro**: Cerro Colorado, 12 km W of Chame, 3000–4000 ft., *Kress et al. 86-1949* (MO, SEL); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69069* (L, MEXU, MO, P, US); near Continental Divide, 9.4 mi. from Chame, ca. 1700 m, ca. 8°35′N, 81°45′W, *McPherson 8918* (CAS, MO); Fortuna Dam area, along trail on Continental Divide, ca. 1200 m, *McPherson 9031* (MO). **Bocas del Toro-Chiriquí**: Chiriquicito–Calderas, Elfin forest, at Divide, on trail, *Kirkbride & Duke 975* (MO); Cerro Colorado, 1300–1400 m, 8°35′N, 81°50′W, *McPherson 13640* (MO, NY). **Chiriquí**: Cerro Colorado, 20 mi. N of Río San Félix, 1660 m, 8°30′N, 81°46′W, *Croat 74987* (MO, US); 1110–1750 m, 8°35′N, 81°54′W, *Hammel & Trainer 14932* (MO); Boquete region, SW slope of Cerro Pate Macho, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66382* (MO, QCA, SCZ); Fortuna Dam area, Fortuna Lake–Chiriquí Grande, 4.5–5 km N of dam over Fortuna Lake, 1100–1134 m, 8°43′N, 82°17′W, *Croat & Grayum 59979* (AAU, B, CM, GH, K, MO, RSA); Gualaca–Chiriquí Grande, 4.8 mi. beyond IRHE facilities at Dam, 4 mi. N of bridge over Bayano Lake, 8°46′N, 82°16′W, *Croat 68027* (COL, G, MEXU, MO).

Philodendron cretosum Croat & Grayum, sp. nov. TYPE: Panama. Coclé: vicinity El Valle de Antón, at forested flat area near Finca Macarenita at La Mesa, 800 m, 8°36′N, 80°07′W, 6 July 1994, *Croat & Zhu 76661* (holotype, MO–04619350–51; isotypes, AAU, B, CAS, CM, COL, CR, F, K, L, M, MEXU, NY, OOM, P, PMA, QCA, SEL, TEX, US, VEN). Figures 125, 126, 144.

Planta epiphytica aut hemiepiphytica; internodia brevia, 1–3 cm diam.; succus calcareus, in sicco mox calcareus; cataphylla 23–42 cm longa, obtuse 1-costata, in sicco pallide flavibrunnea, persistentia ut fibrae pallidae; petiolus obtuse et late aut profunde et anguste sulcatus adaxialiter, 10.5–23.5 cm longus, 3–6 mm diam.; lamina linearis vel oblanceolata, 29–84.5 cm longa, 5–12 cm lata; inflorescentia 1–3; pedunculus (2.5)4–8.9 cm longus, ca. 10 mm diam.; spatha 9–13.5 cm longa; lamina spathae extus pallide viridi vel viridialba, intus viridialba; tubo spathae extus viridi, intus albo; pistilla 4-locularia; loculi cum 18–20-seminibus.

Epiphytic or hemiepiphytic; stem appressed-climbing, elongate, sap chalk-white; internodes short, 4–9 cm long on lower stems, short on flowering plants, 1–3 cm diam., as broad as long or slightly longer than broad, gray-green; roots drying dark brown, few per node; cataphylls thin, membranous, 23–42 cm long, bluntly 1-ribbed, green, drying pale yellowish brown, persisting as pale fibers; **petioles** 10.5–23.5 cm long, 3–6 mm diam., medium green, semiglossy, bluntly and broadly or deeply and narrowly sulcate adaxially, with adaxial margins obtuse or sometimes acute; **blades** linear to oblanceolate, chartaceous to weakly subcoriaceous, weakly bicolorous, drying greenish to yellowish brown on both surfaces, matte and paler below, acuminate to weakly acute at apex (the acumen apiculate), attenuate at base, 29–84.5 cm long, 5–12 cm wide (5.1–8.3 times longer than wide), (2.6–4.7 times longer than petiole), much longer than petioles, broadest in upper one-third; midrib prominently and narrowly sunken above, thicker than broad, bluntly acute, glossy and darker than surface below; basal veins lacking; primary lateral veins 6–9 per side, departing midrib at a 25–45° angle, straight to weakly arcuate to the margins, sunken above, convex below; interprimary veins sunken above, slightly raised below; minor veins arising from midrib only; tertiary veins visible, darker than surface below. INFLORESCENCES 1–3 per axil; peduncle (2.5)4–8.9 cm long, ca. 10 mm diam., drying 3–5 mm diam., shorter than petiole, subterete or irregularly angled, white-striate; **spathe** subcoriaceous, semiglossy, 9–13.5 cm long (1.8–3.3 times longer than peduncle), moderately constricted midway or just below the middle, abruptly acuminate at apex; spathe blade lanceolate, pale green to greenish white outside, 5.5–8 cm long, greenish white inside; spathe tube ellipsoid, green, short white lineate outside, 3.5–5.5 cm long, 1.8–2 cm diam., white (at anthesis) inside; **spadix** stipitate to 5 mm long; 11–15 cm long; pistillate portion white to pale greenish, weakly ellipsoid, 3–3.5 cm long; staminate portion 4.5–7.8 cm long; fertile staminate portion white; sterile staminate portion 1.2 cm diam.; pistils 0.6–0.9 mm long, 3 mm diam., drying blackish; ovary 4-locular, with axile placentation; ovules ca. 20 per locule, 2–3-seriate, 0.3–0.4 mm long; funicle ca. 0.4 mm long, adnate to lower part of partition, style similar to style type D; style apex flat, with a small style boss; stigma hemispherical; the androecium oblong, 3–5-sided, 0.8–1.2 mm long, 0.4–0.6 mm diam. at apex; sterile staminate flowers irregularly 4–6-sided, 1.5–2.1 mm long, 0.7–1 mm wide. INFRUCTESCENCE 6 cm long, 2.5 cm diam.; seeds 18–20 per locule, obovoid to weakly ellipsoid, 0.8–1 mm long, 0.4–0.5 mm diam.

Flowering in *Philodendron cretosum* occurs in both Costa Rica and Panama from March through July (except May), mid-dry season to early rainy season. It probably flowers over a broader period

because post-anthesis collections have been made in January, April, June, July, and November. The post-anthesis collection in January means that the species may have flowered later than July or that there is some bimodality in the flowering. Immature fruits have been collected in November.

Philodendron cretosum ranges from Costa Rica to Panama, from near sea level to 900 m elevation in *Tropical wet forest* and *Premontane rain forest* life zones. The species is perhaps restricted to the Atlantic drainage but has been collected principally from areas along the Continental Divide in Panama.

Philodendron cretosum is a member of *P.* sect. *Philodendron* subsect. *Canniphyllum.* This species is recognized by its short internodes, white chalky sap (hence the name "cretosum," meaning "full of chalk"), persistent, thin, pale cataphyll fibers, bluntly sulcate petioles much shorter than the blades, and especially its linear to oblanceolate blades. Few other species in Central America have white chalky sap, and no other species with white sap have narrow, non-cordate blades.

Philodendron cretosum is not easily confused with any other species in Central America. It resembles *P. tenuipes* Engl. from Ecuador, which also has elongated blades with acute bases and persistent cataphyll fibers, but that species differs in having blades drying darker brown with the primary lateral veins closer and more numerous (more than 15 pairs) and smaller spathes (usually less than 7.5 cm long).

One collection, *Gómez et al. 19121,* reportedly from the slopes of Volcán Miravalles along the Guanacaste–Alajuela border at about 1500 m, would be well above the confirmed elevational range and in a *Lower Montane rain forest* life zone. It is doubtful if it was collected in this life zone or at that elevation. Neither Mike Grayum nor I have encountered this species above 600 m in Costa Rica.

Additional specimens examined. COSTA RICA. **Alajuela**: Reserva Biológica Monteverde Río Peñas Blancas, 500–800 m, *Bello 1070* (CR, MO); 950 m, *1092* (INB, MO); Naranjo–Aguas Zarcas, along Highway 15, 8.5 km NE of Villa Quesada, 600 m, *Croat 46978* (MO); Cañas–Upala, 4 km NNE of Bijagua, Río Zapote, 400 m, *Croat 36295* (MO); San Ramón, *Bittner & G. Herrera 2128* (CR). **Guanacaste**: Parque Nacional Guanacaste, Estación Pitilla, 550 m, 11°02′N, 85°25′20″W, *Hammel et al. 17497* (CR, MO); slopes of Miravalles, above Bijagua, *Gómez et al. 19121* (F, MO, US). **Heredia**: Cerros Sardinal, ca. 2–2.5 km N of Chilamate de Sarapiquí, 80–160 m, 10°28′N, 84°04′W, *Grayum et al. 6148* (MO); La Selva Field Station, 50–100 m, 10°26′N, 84°01′W, *Grayum 1894* (MO), *8546* (MO); *Croat 61212* (MO). **Limón**: Barra de Colorado Refugio, Río Chirripocito–Río Sardina, 10–15 m, 10°38′N, 83°45′W, *Grayum 9022* (CR, MO); Río Segundo, Asunción, Estribaciones Fila Matama, Cerro Matama, 300 m, *Gómez et al. 23424* (MO). PANAMA. **Coclé**: 9.4 km above El Copé, 750–900 m, *Croat 44743* (MO); El Valle region, La Mesa, above El Valle de Antón, 860–900 m, 8°38′N, 80°09′W, *Croat 37344* (F, MO); 800–900 m, *67123* (F, MO, US); *13344* (MO); 775 m, *Croat 74782* (M, MO); 900–1000 m, 8°40′N, 80°07′W, *Knapp 5799* (MO, NY). **Colón**: Nuevo Tonosí–Río Indio, ca. 0 m, *Croat 33555* (MO). **Panamá**: Cerro Campana, 400 m, *Hutchison & Dressler 2974* (BH, F, M, US); *Croat 17164* (F, MO, PMA); 150 m, *35985* (MO); 780–875 m, *25254* (MO); 800 m, 8°41′N, 79°56′W, *74775* (MO); Cerro Jefe region, 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68697* (MO); along road to summit, 750–800 m, 9°14′N, 79°22′W, *Croat 67090* (MO); El Llano–Cartí, 6.8 mi. from the highway, 350 m, *Croat 49123* (MO); Campamento de los guardabosques de INRENARE, 800–900 m, 8°40′N, 79°55′W, *Correa et al. 9516* (STRI). **San Blas**: Nusagandi, km 19.1, *de Nevers & Herrera 7950* (MO). **Veraguas**: Santa Fe region, Escuela Agrícola Alto Piedra–Río Dos Bocas, 5–8 km from school, 730–770 m, *Croat 25910A* (MO).

Philodendron davidsonii Croat, Aroideana 6: 39–41. 1983. TYPE: Costa Rica. Limón: N of Siquirres, originally collected by Jim Tally of Miami, Florida, *Croat 52232A* (holotype, MO–3000000–1; isotypes, B, COL, CR, K, MEXU, NY, US). Figures 10, 129, 130, 136.

Epiphytic climber, often occurring high in canopy; sap clear; stem appressed-climbing, thick, creeping, leaf scars conspicuous, 1.5–2 cm long, 1–3 cm wide; internodes short, thick, broader than long, 1.5–5 cm long, 3–9 cm diam., olive-green to gray-green, becoming tannish white to brownish, scurfy; epidermis peeling and cracking with age; roots few per node, to 7 mm diam., light reddish brown, drying dark reddish brown, smooth, epidermis peeling; cataphylls soft, 28–54 cm long, unribbed to bluntly ribbed to sharply 2-ribbed near apex, green to reddish, sometimes dark green-striate, promptly deciduous; **petioles** 50–85 cm long, 1–2 cm diam., thicker than broad, obtusely V-shaped, broadly sulcate adaxially, rounded abaxially, with adaxial margins sharp, surface medium to dark green-striate with a weak maroon to dark green ring around apex; **blades** ovate-oblong, coriaceous, acute to ± acuminate at apex (the acumen inrolled), subcordate to cordate at base, 50–76 cm long, 21–43 cm wide (1.7–2.6 times longer than wide), upper surface dark green, semiglossy to glossy, lower surface matte, much paler (often tinged purplish violet when young); margins hyaline to yellowish green, sometimes revolute; anterior lobe 48–77.5 cm long, 20–50 cm wide (3.4–6.3 times longer than posterior lobes); posterior lobes 9–19 cm long, 9.6–17.8(24) cm wide, rounded; midrib flat to weakly raised, yellowish green to cream, paler than surface above, convex, weakly striate, pal-

er than surface below; basal veins (1)3–6, mostly 4 per side, with 1–2 (or sometimes all) free to base, 4th to 6th veins coalesced 3–4 cm; posterior rib 0.8–4 cm long, not at all naked or naked to 4 cm; primary lateral veins (10)18–21 per side, departing midrib at a 50–75° angle, straight or weakly arcuate to the margins, sunken to weakly quilted and paler than surface above, convex to raised and paler than surface below; interprimary veins weakly sunken and paler than surface above, weakly raised and darker than surface below; minor veins darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES ± erect, 1–3 per axil; peduncle (3.5)5–9 cm long, 7–27 mm diam., flattened adaxially, pale green to reddish green, or white, often dark green-striate; **spathe** coriaceous, 15–27 cm long ((2.1)2.9–4.6 times longer than peduncle), weakly constricted near the middle (opening 16.5 cm long); spathe blade at anthesis pale green, pale speckled, with margins reddish pink outside, 10–19 cm long, 2–6 cm diam. (the opening to 9 cm long), tinged reddish to maroon (B & K red-purple 2/7) inside; spathe tube pale green, minutely white-short-lineate outside, 5.9–14 cm long, 3–5.5 cm diam., reddish to maroon (B & K red-purple 10/3 to 2/10) inside; **spadix** sessile or weakly stipitate; tapered, 14.5–25 cm long, tapered, broadest near the base; pistillate portion green to yellow-green, slightly tapered toward the apex to cylindrical, 3.3–10 cm long, 1.1–2.5 cm diam. at apex, 1.4–1.7 cm diam. at middle, 1.5–3 cm wide at base, with 19–25 flowers per spiral; staminate portion 9.2–20 cm long; fertile staminate portion creamy white, becoming orange-red (post-anthesis), tapered, 1.6–2.8 cm diam. at base, 1.5–2 cm diam. at middle, 7–12 mm diam. ca. 1 cm from apex, broadest at the base, narrower than the pistillate or sterile portions; sterile staminate portion narrower than the pistillate portion, white, 17–28 mm diam.; pistils 3.3–4.7 mm long, 1.6–2.5 mm diam.; ovary 8–14-locular, 3.7–4 mm long, 2–2.6 mm diam., with sub-basal placentation; ovules 4–8(12) per locule, striate, 2-seriate, usually contained within translucent ovule sac, 0.2–0.6 mm long, about equal in length or shorter than funicle; funicle 0.2 mm long, style 1.2–2.3 mm long, 1.6–2.1 mm diam., similar to style type B or D; style apex usually flat; style apex flat or with a broad boss, pronounced (with divot in center); stigma subdiscoid to globular, unlobed to weakly lobed, 1.8–1.9 mm diam., 0.3–0.7 mm high, covering entire style apex, depressed medially; the androecium truncate, margins 4–6-sided; thecae elliptical to oblong-obovate, 0.1 mm wide; sterile staminate flowers blunt, 4–5-sided, 3.5–4.5 mm long, 1.5 mm wide. Berries greenish (nearly ripe).

Philodendron davidsonii ranges from Costa Rica (no doubt into adjacent southeastern Nicaragua as well) to Panama on the Atlantic slope, from near sea level to about 200 m elevation in *Premontane wet forest* and *Tropical wet forest* life zones.

Philodendron davidsonii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata.* This species is characterized by its generally short-creeping habit often high in the canopy (reportedly to 30 m); short, thick internodes; sharply two-ribbed cataphylls, which are deciduous intact; long, stout, broadly sulcate petioles; large ovate-oblong blades with many sunken primary lateral veins; and one to three inflorescences per axil with the coriaceous spathes green outside and reddish to maroon within.

Philodendron davidsonii has two subspecies; the typical subspecies is found throughout the range of the species, and *P. davidsonii* subsp. *bocatoranum* is known only from the type locality in Bocas del Toro Province.

KEY TO THE SUBSPECIES OF *PHILODENDRON DAVIDSONII*

Base of blade cordate to subcordate; primary lateral veins 16–21 per side, arising at 65–75° angle; Costa Rica to Panama, 0–100 m elevation ..... subsp. *davidsonii*

Base of blade acute; primary lateral veins 10–16 per side, arising at 50–55° angle; Panama (Bocas del Toro), 190–220 m elevation ..... subsp. *bocatoranum*

Philodendron davidsonii Croat subsp. **davidsonii**

Internodes 1–5 cm long, 3–8 cm diam.; cataphylls 38–54 cm long, sharply 2-ribbed; **petioles** 56–85 cm long, obtusely V-shaped, broadly sulcate adaxially, with adaxial margins sharp, with a dark ring at apex; blades 49.5–67 cm long, 21–43 cm wide; basal veins 3–6, mostly 4 per side, with 1–2 free to base, 4th to 6th veins coalesced 3–4 cm; posterior rib 0.8–4 cm long, not at all naked to 4 cm; primary lateral veins (16)18–21 per side, departing midrib at 65–75° angle. INFLORESCENCES 1–3 per axil; peduncle (3.5)5–9 cm long, flowers with style similar to style type D; style apex usually flat with a broad style boss bearing a medial divot; stigma subdiscoid to globular, weakly lobed. Berries greenish, nearly ripe.

Flowering in *Philodendron davidsonii* subsp. *davidsonii* occurs in the late dry season and early wet season with post-anthesis collections from March through August (except April) and immature fruiting collections from June and November. Cultivated collections at the Missouri Botanical Garden flowered in April, May, June, and July.

Philodendron davidsonii subsp. *davidsonii* ranges from northeastern Costa Rica (no doubt into southeastern Nicaragua as well) to Panama on the Atlantic slope, from near sea level to about 100 m elevation in *Premontane wet forest* and *Tropical wet forest* life zones. No specimens have been seen in Costa Rica above 100 m elevation.

Additional specimens examined for P. davidsonii *subsp.* davidsonii. COSTA RICA. **Heredia**: La Selva Field Station, ca. 100 m, *Jacobs 2708* (MO), *Grayum 2931* (MO), *2829* (MO). **Limón**: Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson 3956* (CM, F, MO); *7097* (L, MO, RSA), *8782* (MO); Manzanillo de Talamanca, ca. 5 m, 9°38′N, 82°39′W, *Grayum & Burton 4326* (MO); Refugio Barra del Colorado, between Río Chirripocito and Río Sardina, 12 m, 10°38′N, 83°45′W, *Grayum 9807* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam–Chiriquí Grande, 10 mi. below the divide off highway 1.2 mi., 300–400 ft., *Kress et al. 86-1992* (MO, SEL).

Philodendron davidsonii subsp. **bocatoranum** Croat, subsp. nov. TYPE: Panama. Bocas del Toro: Ojo de Agua, 7 km W of Almirante, 190–220 m, 9°16′N, 82°28′W, 4 Aug. 1976, *Croat 56853* (holotype, MO–3636098–99). Type live at MO. Type plant is a re-collection of a sterile live collection vouchered as *Croat 38177* on 8 July 1983. Figures 19, 131–135.

Internodia 4–9 cm diam.; cataphylla obtuse vel acute 2-costata, persistentia intacta nodis superioribus, tum decidua aut semi-intacta basi; petiolus complanatus vel acute sulcatus adaxialiter, 50.5–67 cm longus; lamina 58–76.5 cm longa, 25–35 cm lata; inflorescentia 2; pedunculus 5.5–6 cm longus; spatha 23–25 cm longa.

Internodes 1–2 cm long, 4–9 cm diam.; cataphylls 28–45 cm long, ca. 6 cm wide, unribbed to bluntly ribbed to sharply 2-ribbed near apex, persisting semi-intact at base; **petioles** 50.5–67 cm long, flattened to sharply sulcate adaxially with adaxial margins conspicuous and erect, maroon ring at apex weakly apparent; **blades** 58–76.5 cm long, 25–35 cm wide; basal veins 1–4, prominently ascending, all free to base or weakly coalesced at base to 1 cm; primary lateral veins 10–16 per side, departing midrib at 50–55° angle. INFLORESCENCES 2 per axil; peduncle 5.5–6 cm long; **spathe** 23–25 cm long; flowers with style similar to style type B, lacking a boss; style apex flat; stigma subdiscoid, unlobed. Berries not seen.

Flowering in *Philodendron davidsonii* subsp. *bocatoranum* occurs during July (based on only two collections).

Philodendron davidsonii subsp. *bocatoranum* is endemic to Panama, known only from the type locality in Bocas del Toro, at 190 to 220 m elevation in *Premontane wet forest.*

The taxon is distinguished by its thick, short internodes, two-ribbed, deciduous cataphylls, long, sharply sulcate petioles, and ovate-oblong blades acute at the base.

Philodendron davidsonii subsp. *bocatoranum* differs from the typical subspecies in having blades acute rather than decidedly lobed at the base and 11 or fewer primary lateral veins (vs. about 16 or more) arising at more acute angles with the midrib (50–55° vs. 65–75°).

Additional specimen examined. PANAMA. **Bocas del Toro**: vic. of Ojo de Agua, 7 km W of Almirante, 190–220 m, 9°06′N, 82°28′W, *Croat 38177* (CAS, HUA, M, MO, SCZ, VEN).

Philodendron dodsonii Croat & Grayum, sp. nov. TYPE: Ecuador. Pichincha: along Río Blanco across from Villa Hermosa on road 1.9 km N of main Sto. Domingo de Los Colorados–Esmeraldas Highway, departing main highway 25 km NW of Santo Domingo, 410 m, 0°5′S, 79°15′W, 13 Mar. 1992, *Croat 72982* (holotype, MO–04658574–5; isotypes, AAU, B, COL, R, K, M, MEXU, NY, PMA, QCA, QCNE, US). Figures 137–143, 150.

Planta hemiepiphytica; internodia brevia 2.5–3 cm diam.; cataphylla usque 20–33 cm longa, leniter vel acute 2-costata, interdum incostata, persistentia, demum fibrosa; petiolus subteres, 52–93 cm longus; lamina ovata, 36–87 cm longa, 28–66 cm lata, atriviridis supra, moderate pallidior et nitida infra, in sicco atriflavibrunnea et impolita vel leniter nitida; costa postica manifeste nuda; inflorescentia 2–5; pedunculus 5–9.5(14) cm longus, 6–10 mm diam.; spatha 16–18 cm longa; lamina spathae extus alba, intus rubella; tubo spathae extus rubropurpureo vel atrirubella vel viridi, intus rubro-purpureo vel atrirubello; pistilla (4)5-locularia; loculi ca. 20-ovulati.

Hemiepiphytic; stem appressed-climbing, leaf scars conspicuous, 1–2.7 cm long, 1.5–3.5 cm wide; internodes short on adults, stout, matte to glaucous, 2.5–3 cm diam., frequently longer than broad on nonflowering plants, gray-green, becoming whitish to grayish with age, epidermis flaking; cataphylls thin, spongy, to 20–33 cm long, weakly to sharply 2-ribbed, sometimes unribbed, light green, dark green-striate, persisting in parchment-like mats, eventually fibrous, rarely deciduous intact, margins clear; **petioles** 52–93 cm long, 9–25 mm diam., subterete to obtusely flattened abaxially, soft, drying black, surface pale, dull whitish-streaked, thinly dark green-striate, drying black; **blades** ovate, subcoriaceous, semiglossy, slightly bicolorous, very short acuminate to ± acute at apex, weakly cordate to sagittate at base, 36–87 cm long,

28–66 cm wide (1.3–1.6 times longer than wide), (0.7–1.2 times longer than petiole), about equal in length to petiole, upper surface dark green, drying dark brown to dark yellow-brown, lower surface moderately paler and glossy, drying yellow-brown and matte to weakly glossy, margins weakly undulate and upturned, hyaline; anterior lobe 31–76 cm long, 39–70 cm wide (1.65–2.9(4) times longer than posterior lobes); posterior lobes 11–29 cm long, 9–31 cm wide, broadly rounded to broadly obtuse; midrib flat to sunken, slightly paler than surface above, convex, concolorous below; basal veins 7–8 per side, and with the first free to base, numbers 3–7 coalesced 4–12 cm; posterior rib prominently naked to 6 cm along the sinus; primary lateral veins (4)7–8 per side, departing midrib at a 50–60° angle, to the margins, sunken and paler than surface above, convex to round-raised, usually darker than surface, sometimes paler than surface near base below; interprimary veins sunken and concolorous above, raised and concolorous below; tertiary veins visible, slightly darker than surface below; minor veins darker than surface, drying smooth below, arising from both the midrib and primary lateral veins. INFLORESCENCES 2–5 per axil; peduncles 5–9.5(14) cm long, 6–10 mm diam., subterete, pale green, white-streaked; **spathe** 16–18 cm long ((1)1.8–3.5 times longer than peduncle), moderately constricted above the tube; spathe blade white outside, reddish inside; spathe tube red-purple to dark reddish (B & K red-purple 3/7.5) outside, red-purple to dark reddish inside, sap mango-scented; **spadix** 13–15(18) cm long; pistillate portion 6 cm long in front, 5 cm long in back, 2.5 cm diam. at middle, 2.2 cm wide at base; staminate portion 11 cm long; fertile staminate portion ca. 1 cm diam.; sterile staminate portion 2.5–3 cm diam.; pistils 4 mm long, 1.7–2.3 mm diam.; ovary (4)5-locular, with axile placentation; ovules ca. 20 per locule, 2-seriate, 0.3–0.4 mm long, slightly longer than funicle; funicle 0.2–0.4 mm long, adnate to lower part of partition, style similar to style type B; central style dome fairly well developed; style apex broadly domed; stigma inserted on entire style apex; the androecium truncate, ± prismatic, oblong, margins irregularly 4–5-sided, 1–2.5 mm long; thecae oblong, 0.3 mm wide, contiguous, ± parallel to one another; sterile staminate flowers clavate, irregularly 3–5-sided, 2.3–3.7 mm wide.

Flowering in *Philodendron dodsonii* probably occurs during the rainy season, June–September, in Central America. It is known to flower only during September there, with post-anthesis collections also made from July through September and mature fruits in March. In South America, flowering collections have been made in June and July, post-anthesis from May through September, immature fruiting from February through November (except May, August, and October), and mature fruiting in September.

Philodendron dodsonii is known from Costa Rica and Ecuador and is expected to be found on the Caribbean slope of Panama and probably on the Pacific slope of Colombia. In Costa Rica, it occurs at 240 to 1300 m elevation, principally on the Atlantic slope but also on the Pacific slope on the Fila Costeña in *Tropical wet forest* and especially in *Premontane rain forest* life zones. In Ecuador, this species is known from *Tropical wet forest* life zones at 20 to 1750 m in Pichincha Province.

Philodendron dodsonii is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its stout, short internodes, weakly two-ribbed cataphylls that persist in parchment-like mats and are eventually fibrous; more or less terete petioles; large ovate, yellowish-brown-drying blades with naked posterior ribs; and short-pedunculate spathes with the tube dark green to reddish outside and red within. Another feature useful for determination is the presence of tiny granulations or protuberances on the lower leaf surface. Juvenile blades often have minute pale dots on the surface.

Philodendron dodsonii is most easily confused with *P. dominicalense,* a species with very similar features, which differs in having a single ovule per locule (vs. ca. 20 for *P. dodsonii*) and an outer green spathe tube (vs. red for *P. dodsonii*).

Philodendron dodsonii also appears close to *P. schottianum,* but that species differs in having cataphylls drying with a much thicker, yellowish epidermis and coarser fibers; petioles drying yellowish brown (vs. almost black for *P. dodsonii*); blades drying with raised minor veins (vs. essentially smooth for *P. dodsonii*); and inflorescences usually scarcely constricted above the tube.

Another species that might be confused with *P. dodsonii* is *P. grayumii.* It has blades similar in shape, size, and color upon drying but which differ in having the upper surface glossy upon drying and in usually having laticifers visible on the lower surface, and especially in having mostly free basal veins with the posterior rib (when present) rarely naked along the sinus.

A collection near San Vito and the only wild-collected specimen from the Pacific slope in Costa Rica differs in having longer internodes. It perhaps represents another species, but in other respects it matches well with *P. dodsonii.*

This species was recognized as distinct by Sodiro (in herb.), under the name *P. robustum* Sodiro ined., previously published for a different species by Schott (1860).

Philodendron dodsonii is named in honor of Calaway Dodson, Director of the Centro Científico Río Palenque and staff member of the Missouri Botanical Garden, who first studied the species for the *Flora of Río Palenque* (Dodson & Gentry, 1978). The species was erroneously included in the above-mentioned work as *P. devansayeanum* L. Linden, a poorly known entity purportedly collected in the eastern Andes of Peru. Though the last-mentioned species was poorly described and is represented only by a somewhat stylized painting (but no bona fide herbarium specimens), there is little likelihood that it could be the same as a species occurring on the western slopes of the Andes. The illustration appears to show leaf blades with basically free basal veins and little or no posterior ribs, whereas *P. dodsonii* has well-developed posterior ribs. A collection from Ecuador in Sucumbios (*Croat 50317*) may prove to be this species. Though the inflorescence is immature its blades match those of *P. dodsonii*. Two other collections, *Gentry 71004* from Bolivia (La Paz Province, 1500–1550 m) and *Croat 55455* from Colombia (Cundinamarca Dept., 2000 m), may prove to be *P. dodsonii*. If so, the range statement could be affected.

Additional specimens examined. COSTA RICA. **Alajuela**: Río Sarapiquí, at bridge on road to Colonia Virgen del Socorro, 830 m, 10°16′N, 84°11′W, *Croat 68318* (CR, MO); 17 km NW of San Ramón, 785 m, 10°14′15″N, 84°33′W, *Croat 68138* (MO); Río Cataratitas, ca. 20 km NW of San Ramón, 850 m, 10°12′30″N, 84°32′W, *Grayum et al. 6327* (MO). **Cartago**: Río Reventazón, CATIE, Turrialba, ca. 600 m, 9°54′N, 83°39′W, *Grayum et al. 3820* (MO); along Camino Raiz de Hule, SE of Platanillo (Tsipiri), 1200–1400 m, *Croat 36796* (MO, US). **Heredia**: Zona Protectora La Selva, Río Peje–Río Guácimo, along Quebrada Cantarrana, 300–400 m, 10°22′N, 84°30′W, *Grayum & Jacobs 3592* (CR, MO). **Limón**: Cordillera de Talamanca, along Río Madre de Dios, 240 m, 10°03′N, 83°26′W, *Grayum et al. 8662* (MO); Río Blanco, Río Frio–Limón, W of Guápiles, Quebrada Danta, 3 mi. S of main highway, 360 m, 10°12′N, 83°49′W, *Croat 68422* (CM, MO). **Puntarenas**: Las Cruces Botanical Garden, 1300 m, *Croat 44420* (MO); *44464* (MO); ca. 4 km SE of San Vito, 1150 m, 8°47′30″N, 82°58′W, *Grayum 8112* (INB, MO); Las Cruces Botanical Garden–Río Jaba, ca. 3.5 km SE of San Vito de Coto Brus, ca. 1160–1200 m, 8°47′30″N, 82°58′W, *Grayum 5980* (MO). **San José**: San Isidro del General–Dominical, SW of San Isidro, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35260* (MO); 990–1100 m, *Croat & Hannon 79114* (CR, INB, MO); Tarrazú, vic. Hormiguero, 1100–1200 m, *Croat 78974* (CR, INB, MO).

COLOMBIA. **Valle:** Cali–Buenaventura Highway, 1.2 km E of Cisneros, 220–260 m, *Croat 62829* (COL, MO, NY). ECUADOR. **Cotopaxi**: Quevedo–Latacunga, 3 km E of El Palmar, 800 m, *Dodson & Gentry 10253* (MO); La Mana, 1 km N of Pucayacu, 750 m, *Croat 73276* (MO); 2 km N of Pucayacu near Río San Francisco, 690 m, *Croat 57080* (MO, QCA); Río Guapara, ca. 20 km NW El Corazón, 250 m, *Sparre 17106* (S), *17164* (S), *17150* (S), *17108* (S), *17145* (S); Río Pilaló, Tenefuerste, km 52–53, 750–900 m, *Dodson & Dodson 12914* (MO). **Cotopaxi–Cañar–Chimborazo–Bolívar**: Bucay, 1000–1250 ft., *Camp E-3714* (MO, NY, S), *E-3656* (MO, NY, S). **Cañar**: Azoques–El Triumfo Road, 1 km S of La Delicia, 2°27′S, 79°10′W, *Croat 50867* (MO, QCA). **El Oro**: Piñas–Santa Rosa, above El Placer, 400–700 m, *Harling et al. 15524* (GB); Machala–Loja Road, 890 m, *Croat 50718* (MO, QCA). **Esmeraldas**: Quinindé, Bilsa Biological Station, Montañas de Mache, 35 km W of Quinindé, 5 km W of Sta. Isabela, 400–600 m, 0°21′N, 79°44′W, *Pitman & Marsh 1146* (MO, QCA); Viche, *Asplund 16514* (S); Fila de Bilsa, 7 km E of San José de Bilsa, ca. 80 km SW of Esmeraldas, 12 km SE of El Salto on Atacames–Muisne Road, 280 m, 0°37′N, 79°51′W, *Gentry et al. 72977* (MO); Río Esmeraldas, opposite Quinindé (Rosa Zárate), *Asplund 16361* (S); near San Mateo, 80 m, *Croat 55632* (CAS, GH, MO, QCA); Río Lita, near Lita, 600–650 m, *Croat 38944* (MO). **Guayas**: Teresita, 2 km W of Bucay, 270 m, *Hitchcock 20537* (NY, US); 3 km W of Bucay, 270 m, *Hitchcock 20489* (NY, US), *20440* (US); Cordillera Chongon–Colonche, 600 m, 1°48′S, 80°47′N, *Cornejo & Bonifaz 5237* (GUAY, MO); Huigra–El Triumfo, 160 m, *Croat 61593* (F, MO, QCA). **Imbabura**: 13–15 km E of Lita, 800 m, *Croat 38918* (MO); Cachaco, 9 km E of Lita, 630 m, *Croat 39000* (MO). **Los Ríos**: Babahoyo–Montalve, Hacienda Clementina, 20 m, *Sparre 17966* (S); Centro Científico Río Palenque, 230 m, *Croat 38651* (MO); 250 m, *50658* (MO, QCA); 220 m, 0°35′S, 79°12′W, *73803* (MO, QCA, US). **Pichincha**: Reserva ENDESA, Río Cabayales, ca. 700 m, 0°05′N, 79°02′W, *Croat & Rodríguez 61503* (CAS, CR, MO, NY, QCA); *61516* (CM, MO, PMA, QCA, US); 710 m, 0°03′N, 79°07′W, *Croat 73185* (CM, MO, QCA); Alóag–Santo Domingo, Río Toachi, 850 m, *Sparre 17816* (S); Tinalandia, above Río Toachi, 700 m, *Croat 55745* (MO), *55738* (MO, QCA, SEL); Nono–Nanegal, 13 km SE of Nanegal, 1440 m, *Croat 38895* (MO); Nanegal, *Sodiro 13* (G); 35 km NW of Santa Domingo, Río Blanco, ca. 250 m, *Gentry 9619* (MO); Quito, Parroquia Nanegal, along Río Umachaca near Hacienda El Carmen, 1250 m, 0°07–7.5′N, 78°38′W, *Webster et al. 28781* (DAV, MO); Reserva Maquipucuna, Hacienda Esparragos–Cerro de Sosa, ca. 6 km airline SE of Nanegal, 1500–1600 m, 0°7′N, 78°38′W, *Webster & Bainard 27500* (DAV, MO); Cerro Campana, 5–6 km (airline) E of Nanegal, 1750 m, 0°09′N, 78°37′W, *Webster et al. 30069* (DAV); La Independencia–Río Caoni, 210 m, *Croat 55650* (MEXU, MO, QCA, WIS); Santo Domingo de Los Colorados, Hacienda Zaracay, 500 m, *Sparre 15190* (S), *15191* (S), *15192* (S); Rancho Brahman, ca. 10 km NW of Santo Domingo de los Colorados on road to Esmeraldas, 400 m, *Sparre 14090* (S); El Paraíso–Saguangal Road, 3 km from El Paraíso, 1500 m, 78°46′W, 0°10′N, *Øllgaard et al. 37799* (QCA).

Philodendron dolichophyllum Croat, sp. nov. TYPE: Panama. San Blas: Nusagandi, El Llano–Cartí road, 9 mi. N of main highway, Nergan Igar (Nergan Trail), 350 m, 9°20′N, 79°W, 2 July 1994, *Croat & Zhu 76569* (holotype, MO–4619523–25; isotypes, B, COL, CR, F, K, NY, PMA, US, VEN). Figures 145–148, 151.

Planta plerumque hemiepiphytica; internodia 4–6 cm longa, 2.5–4 cm diam.; cataphylla usque 20–60 cm longa, acute 2-costata, decidua; petiolus subteres, 28–41 cm longus, 7–20 cm diam.; lamina oblongo-lanceolata, anguste rotunda vel leniter subcordata basi, 53–75 cm longa, 12–15.2 cm lata, in sicco rubrobrunnea; nervis lateralibus I 17–20 utroque; inflorescentia 2–3; pedunculus 9–12.5 cm longus, 5–17 mm diam.; spatha 14–20 cm longa; lamina spathae extus viridi vel purpurescenti, intus albida; tubo spathae extus purpureo aut marronino, intus purpureo vel rubello; pistilla 6–8(9)-locularia; loculi 3–7-ovulati; baccae aurantiacae.

Hemiepiphytic, rarely terrestrial on steep banks; stem appressed-climbing, to 3 m long, elongate, leaf scars conspicuous, 1–1.4 cm long, 1–1.3 cm wide; roots few, dark yellow-green, faintly ridged, becoming reddish brown, semiglossy, to ca. 30 cm long, 3–4 mm diam.; internodes short, semiglossy, somewhat scurfy, 4–6 cm long, 2.5–4 cm diam., as long as broad or slightly longer than broad, dark green, drying brown; cataphylls coriaceous, 20–60 cm long, sharply 2-ribbed, pale greenish white, sometimes with reddish base, drying red-brown, deciduous. LEAVES erect-spreading to spreading, the lowermost somewhat pendent; **petioles** 28–41 cm long, 7–20 mm diam., subterete, somewhat obtusely flattened adaxially, weakly glossy, moderately spongy, dark green to gray-green with a moderately conspicuous dark ring at apex, drying brownish; **blades** large oblong-lanceolate, subcoriaceous to weakly coriaceous, acuminate to gradually acuminate at apex, gradually tapered toward base or narrowly rounded to weakly subcordate at base, 53–75 cm long, 12–15.2 cm wide (4.4–4.9 times longer than wide), (1.6–2.3 times longer than petiole), broadest at or near middle, upper surface medium green, moderately bicolorous, drying reddish brown, semiglossy, lower surface semiglossy, paler; midrib raised to slightly convexly raised to broadly convex, paler than surface when fresh, drying darker than surface above, rounded, somewhat thicker than broad to acute, paler than surface below; basal veins lacking; primary lateral veins 17–20 per side, departing midrib at a 70–80° angle, slightly arcuate to margin, weakly sunken to moderately obscure above, weakly raised and paler than surface below; interprimary veins slightly less conspicuous than primary lateral veins; minor veins distinct, prominently visible below upon drying, arising from the midrib only. INFLORESCENCES 2–3 per axil; peduncle 9–12.5 cm long, 5–17 mm diam., medium green, minutely white striate, clearly demarcated from the colored spathe; **spathe** coriaceous, 14–20 cm long (1.6–1.85 times longer than peduncle), acute at apex; spathe blade green to purplish outside, whitish inside; spathe tube oblong-ellipsoid, purple or maroon outside, purple to reddish inside; **spadix** sessile, (6)9.5–19 cm long, broadest near the base or above the middle; pistillate portion cylindrical to ellipsoid, 3.2–5.8 cm long, 1.1–1.5 cm diam. at apex, 1.1–1.7 cm diam. at middle, 1.1–1.2 cm wide at base, with 15–17 flowers visible per spiral; staminate portion 6–9.8 cm long; fertile staminate portion white, tapered to clavate, 8–11 mm diam. at base, 7–10 mm diam. at middle, 5–18 mm diam. ca. 1 cm from apex, narrower than or as broad as the pistillate portion; sterile staminate portion as broad as the pistillate portion, 8–11 mm diam.; pistils 1.4–3 mm long, 8–25 mm diam.; ovary 6–8(9)-locular, 9–25 mm diam., with sub-basal, sometimes basal placentation; ovule sac 0.5 mm long; ovules 3–7 per locule, contained within transparent ovule sac, 0.1–0.9 mm long, almost equal in length to funicle, style similar to style type B; style apex flat; stigma discoid, unlobed, 0.6–1.3 mm diam., 0.1–0.4 mm high, covering center of style apex; the androecium truncate, irregularly 4–6-sided, 0.4–0.8 mm diam. at apex; thecae ovate or oblong, 0.2 mm wide; sterile staminate flowers irregularly blunt, 1–2 mm long, 1 mm wide. INFRUCTESCENCE with berries orange, narrowly ovoid-ellipsoid, tapered and obscurely beaked at apex, 1.2 mm long, 9 mm diam.; seeds 2–3 per locule, 0.8–2.8 mm long, 0.2–2.5 mm diam.

Flowering and phenology in *Philodendron dolichophyllum* are unclear. Flowering collections have been made in February, June, and August, with post-anthesis collections from March, July, August, and October, and immature fruiting collections from March, June, July, and September.

Philodendron dolichophyllum is endemic to Panama (though to be expected in eastern Costa Rica), from 325 to 650 m elevation in *Tropical wet forest* life zones.

Philodendron dolichophyllum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. This species is distinguished by its appressed-climbing habit with at least the apical internodes short; sharply two-ribbed, deciduous cataphylls; subterete petioles (about half as long as the blade); and especially by its long, slender spreading leaf blades (hence the name "dolichophyllum"), which dry typically reddish brown and have weakly sunken primary lateral veins.

Philodendron dolichophyllum is not easily confused with any other species in Central America, but bears a superficial resemblance to *P. pseudauriculatum* with which it may occur. Both species have petioles and blades of comparatively equal

lengths and spathes clearly demarcated from the peduncle. *Philodendron pseudauriculatum* differs in having proportionately much shorter leaves with blades that dry gray-green and have prominently sunken primary lateral veins. In addition, the outer surface of the spathe tube in *P. dolichophyllum* is typically maroon or purple, while the blade is green to purplish. *Philodendron pseudauriculatum* has the spathe tube white to pinkish white at anthesis.

Philodendron dolichophyllum might also be confused with *P. auriculatum*, which differs in having proportionately longer petioles and blades drying mostly yellow-green and with a lower blade length/petiole ratio (1.4–1.6 vs. 1.6–2.3 times longer than petiole) than *P. dolichophyllum*. In addition, the spathe of *P. auriculatum* is yellowish green outside and not clearly demarcated from the peduncle (clearly demarcated from peduncle in *P. dolichophyllum*).

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, road to Chiriquí Grande, N of Fortuna Dam, 650–700 m, 8°45′N, 82°15′W, *McPherson 11136* (MO). **Coclé**: El Copé region, Alto Calvario, 200–400 m, 8°45′N, 80°35′W, *Hamilton & Davidse 2638* (MO). **Panamá**: El Llano–Cartí, 10.1 mi. N highway, 325–350 m, 3°20′N, 78°58′W, *Croat 67350* (F, MO, RSA, US); Mile 12, 200–500 m, *Croat 22908* (F, DUKE, MO, NY); Mile 7, 460 m, 9°19′N, 79°59′W, *Croat 75112* (MO); Km 18, 900–1000 ft., 9°16′N, 78°58′W, *Sytsma 1068* (MO); ca. 16–18 km N, 400 m, *Tyson & Nee 7359* (L, MO, QCA); El Llano–Cartí, near Nusagandi, 300–400 m, 9°20′N, 79°W, *Hamilton & Stockwell 1075* (MO). **San Blas**: Nusagandi–Cartí, 400 m, 9°18′N, 78°58′W, *McDonagh et al. 126* (BM, MO); El Llano–Cartí, 23–29 km N of Pan-American Hwy, 300–400 m, 9°22′N, 78°69′W, *Knapp 1878* (M, MO, NY); Km 22, 350 m, 9°19′N, 78°55′W, *de Nevers & Herrera 7849* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río San Luis, past Escuela Agrícola Alto de Piedra, at Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66895* (CM, MO, PMA, SAR).

Philodendron dominicalense Croat & Grayum, sp. nov. TYPE: Costa Rica. San José: along road between San Isidro del General and Dominical, ca. 4.8 mi. E of Río Pacuar, ca. 1000 m, ca. 9°19′N, 83°46′W, 22 May 1976, *Croat 35268*, (holotype, MO–2395109, MO–2395111). Figures 153, 154.

Planta hemiepiphytica; internodia 2.5–10 cm longa, 2–5 cm diam., cano-viridia, in sicco flavibrunnea; cataphylla mollia, 16–29 cm longa, leniter vel acute 2-costata, persistenta semi-intacta; petiolus subteres, 37–74 cm longus, 1.5–2 cm diam.; lamina ovato-cordata, 41–46 cm longa, 19–37.5 cm lata, in sicco atribrunnea; costa postica haud nuda aut usque 2.5 cm; inflorescentia 2; pedunculus 8–9 cm longus; spatha 14–14.5 cm longa, omnino viridis; pistilla 5–6-locularia; loculi 1-ovulati.

Hemiepiphytic; internodes coarsely white-striate beneath each node, somewhat soft, drying semiglossy, 2.5–10 cm long, 2–5 cm diam., gray-green, drying yellow-brown, epidermis fissured closely; roots moderately few per node, to ca. 30 cm long, drying 2–3 mm diam., reddish brown, semiglossy, sharply ridged; cataphylls soft, 16–29 cm long, weakly to sharply 2-ribbed, green to pale red, drying thin, brown, persisting semi-intact at upper nodes; **petioles** 37–74 cm long (averaging 51 cm long), 1.5–2 cm diam., subterete, weakly spongy, medium green, weakly flattened near apex adaxially, surface light green streaked; **blades** ovate-cordate, acuminate at apex, prominently lobed at base, 41–46 cm long, 19–37.5 cm wide (1.1–1.7 times longer than wide), upper surface dark green, semiglossy to weakly glossy, drying dark brown, lower surface semiglossy, much paler, drying yellow-brown; posterior lobes rounded, 12.5–15 cm long, about as broad as long; sinus hippocrepiform, 8–11 cm deep; midrib flat to raised, paler than surface above; basal veins 5–6 per side, with the uppermost free to base, second basal vein coalesced no more than 1 cm, (2)3–4 coalesced 2.5–5 cm; posterior rib not at all naked or naked up to 2.5 cm; primary lateral veins 4–6 per side, raised or sunken, darker than surface, drying dark brown below; interprimary veins in part sunken, the remainder flat but visible below; minor veins alternately strongly or weakly visible, with the more prominent veins weakly stitched below, arising from both the midrib and primary lateral veins. INFLORESCENCES 2 per axil; peduncle 8–9 cm long, 1–1.5 cm diam., fleshy, drying dark brown; **spathe** 14–14.5 cm long, weakly constricted above the tube, green throughout, narrowly acuminate at apex, drying dark brown outside; spathe tube 5.5–6.5 cm long, 2–2.3 cm diam.; **spadix** sessile; to 11.7 cm long; pistillate portion cylindrical, broadest midway, 1.2–1.3 cm diam., weakly tapered in both directions; staminate portion 8.5–9 cm long; fertile staminate spadix broadest at sterile portion, constricted to 9–10 mm ca. 1.5 cm above base, then clavate upward, bluntly tapered at apex, 10–11 mm diam. in upper one-third, 7–8 mm diam. 1 cm from apex; sterile staminate portion 12–13 mm diam.; pistils 1.6 mm long; ovary 5–6-locular, 0.9 mm diam., with sub-basal placentation; ovules 1 per locule, contained within transparent, gelatinous matrix (no true envelope), 0.3–0.4 mm long, longer than funicle; funicle 0.2–0.3 mm long, with a tuft of trichomes near base, style 0.7 mm diam., similar to style type B; style apex flat to concave; the androecium truncate, ± prismatic, margins mostly irregularly 5-sided, 0.7–1.1 mm long; thecae oblong, 0.4 mm wide, ± parallel to one another, contiguous.

PREADULT leaves with petioles 17–20 cm long; blades to 31 cm long and 15 cm wide.

Flowering phenology of *Philodendron dominicalense* is unclear owing to its rarity, but since it was found in flower in May, during the early wet season, it probably flowers and fruits in the wet season.

Philodendron dominicalense is endemic to southwest Costa Rica on the Pacific slope in the vicinity of the type locality along San Isidro–Dominical road, at ca. 1000 m, in *Premontane rain forest.*

Philodendron dominicalense is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is distinguished by its appressed epiphytic habit; thick grayish green stems with internodes mostly longer than broad; soft, weakly 2-ribbed, semi-persistent, intact cataphylls; subterete petioles about as long as the blades; ovate-cordate brown-drying blades with the posterior ribs naked for a short distance to the sinus; and paired short-pedunculate inflorescences with green outer spathe surfaces and one ovule per locule.

Philodendron dominicalense is vegetatively almost identical to *P. dodsonii,* but that species differs in having the spathe red-purple to dark reddish outside and ovaries with axile placentation and about 20 ovules per locule (vs. spathe tube green outside, ovaries with basal to sub-basal placentation, and 1 ovule per locule). *Philodendron dodsonii* also differs in usually having persistent fibrous cataphylls, a sunken upper midrib (vs. flat to raised), and posterior ribs usually prominently naked for 6 cm (vs. not at all naked or naked to only 2.5 cm).

This species is also similar to *P. schottianum,* especially in shape and color of the dried blades. The latter species differs in having shorter internodes with thicker cataphylls, which dry yellow and weather promptly into a coarse network of fibers (vs. persisting semi-intact at upper nodes then deciduous).

Additional specimen examined. COSTA RICA. **San José**: San Isidro del General–Dominical, SW of San Isidro, 6 mi. from Río Pacuare, 1000 m, *Croat 35454* (MO).

Philodendron dressleri G. S. Bunting, Ann. Missouri Bot. Gard. 50: 25. Fig. 2. 1963. TYPE: Mexico. Nayarit: Tepic–San Blas, along Hwy. 54, 14–16 mi. SW of junction with Hwy. 15 (Tepic–Mazatlán), 75 m, 5 Sep. 1961, *Moore & Bunting 8688* (holotype, BH; isotypes, K, MO, US). Figures 152, 157–160.

Hemiepiphytic; stem scandent, 3–3.5 cm long, 4–4.6 cm diam., leaf scars conspicuous, 3–3.5 cm long, 4–4.6 cm wide; internodes short, stout, succulent, scurfy, 3–6.5 cm long, 4–7 cm diam., broader than long, pale olive-green to gray-green, becoming grayish white with age, epidermis peeling; roots few per node, brownish, smooth, long, to 7 mm diam.; cataphylls 16–22 cm long, sharply 2-ribbed, drying weakly 2-ribbed, densely short dark striate, sometimes deciduous in dry season; **petioles** 34.5–70 cm long, 1–1.8 cm diam., terete, somewhat spongy, surface dark green-striate, dark green ring around apex; **blades** ovate in outline, deeply incised-lobate, bipinnatifid, weakly bicolorous, matte to semiglossy, acute to weakly obtuse at apex (the acumen apiculate), cordate at base, 30–46.5 cm long, 27–40.5 cm wide (0.99–1.2 times longer than wide), (0.9–1.2 times longer than petiole), broadest near the middle; anterior lobe 20.5–30 cm long with up to 6 segments, 12–19 cm long and each 3–5-lobed; posterior lobes rounded in outline, turned up at an angle to midrib with ca. 5 similarly lobed segments; sinus closed or nearly so; segments pinnatifid, 12.3–27 cm long, divided to within 2–15 cm from the midrib; the interlobal sinus divided 0.4–0.7 the length of the lobe; midrib flat, dark green-striate, paler than surface above, round-raised, pale striate, paler than surface below; basal veins 4 per side, 3–4 coalesced 5–10 mm; posterior rib naked for 2.5 cm; primary lateral veins 5–6 per side, departing midrib at a 45–60° angle, ± straight, eventually branching to the margins, flat to weakly raised above, round-raised and paler than surface below; reticulate veins visible, darker than surface below; minor veins arising from both the midrib and primary lateral veins; tertiary veins sunken and paler than surface above, raised and paler than surface below. INFLORESCENCES 1 per axil; peduncle 9–16 cm long, 7–9 mm diam. (dried), green; **spathe** 12–21 cm long (1.3 times longer than peduncle), weakly constricted above the middle, ± obtuse at apex; spathe blade dark green outside, pinkish, with darker punctations inside; spathe tube green outside, to 4.5 cm long, purplish violet to wine-red or crimson inside; **spadix** 10–15 cm long; pistillate portion to 3.5 cm long, 2.2 cm diam.; staminate portion to 14 cm long; fertile staminate portion clavate, to 1.9 cm diam. at base, 2.4 cm diam. ca. 1 cm from apex; sterile staminate portion 2.4 cm diam.; pistils 3.7(7) mm long; ovary 4–5-locular, with axile placentation; ovule sac 2.5 mm long; ovules 3–4 per locule, 2-seriate, contained within translucent envelope, 0.4 mm long, longer than funicle; funicle 0.2–0.3 mm long, adnate to lower part of axillary wall, style similar to style type B; central style dome sometimes present; style apex flat; stigma subdiscoid to hemispheroid, 1.8 mm diam., 0.7 mm high, covering entire style apex; the androecium truncate, ±

prismatic, irregularly 5–6-sided, ca. 1.6 mm long; thecae ± oblong, 0.4 mm wide, nearly contiguous, ± parallel to one another. INFRUCTESCENCE with spathe 10–13 cm long, pistillate spadix 4–6.5 cm long, 3.5–4 cm diam.; seeds 3–4 per locule, 2 mm long, 0.8 mm diam.

Flowering in *Philodendron dressleri* is probably during the rainy season. Post-anthesis collections are known from July and September with immature fruiting collections known from December and January.

Philodendron dressleri is endemic to west-central Mexico from coastal Nayarit including Tres Marías Islands (off the western coast of Mexico) to southern Sinaloa, from sea level to 370 m elevation in "Selva Baja Caducifolia."

Philodendron dressleri is a member of *P.* sect. *Polytomium.* This species is characterized by its stout, succulent stems with short internodes, weakly two-ribbed, deciduous cataphylls, terete, somewhat spongy petioles (about as long as the blades), bipinnatifid blades divided about midway to the midrib, and solitary green inflorescences with the spathe tube purplish violet to wine-red within.

Philodendron dressleri is the most northerly-ranging species of *Philodendron,* extending almost to the Tropic of Cancer. It is probably most closely related to *P. warszewiczii,* but is also similar to *P. radiatum,* both of which differ in having gradually much more deeply divided (almost to the midrib) blades (vs. pinnatifid 0.4–0.7 the way to the midrib in *P. dressleri*). *Philodendron warszewiczii* ranges from Honduras to western Mexico, but no further north than the state of Jalisco. *Philodendron radiatum* ranges no further north than Chiapas on the Pacific slope.

The species is superficially most similar to *P. radiatum* var. *pseudoradiatum,* which also has blades divided less than halfway to the midrib. However, that taxon differs in comprising more scandent plants with slender stems having internodes longer than broad (2–12 × 1–2.5 cm for *P. radiatum* var. *pseudoradiatum* vs. 3–3.5 × 4–4.6 cm for *P. dressleri*).

For an additional photo of this species see Bunting (1965: 332).

Additional specimens examined. MEXICO. **Nayarit**: near Sangaite, E of San Blas, *Philbrick 414* (BH); Tepic–Puerto Vallarta, along Hwy. 200, 33 mi. S of Tepic, 4 mi. N of Las Varas, 370 m, *Croat 45360* (CM, MO); 6 mi. S of Mazatan, *Dressler & Wirth 2732* (UC, US); W of Jalcocotán, *Dressler 1051* (UC); 5–6 mi. E of San Blas along highway, *Gentry et al. 19477* (US); Tres Marías Islands, María Madre, *Ferris 6249* (DS, US). **Sinaloa**: Labradas vic., *Ferris & Mexia 5290* (CAS, DS); Culiacán, *González-Ortega 6632* (US); Mpio. Concordia, Sindicatura Mesillas, Cañada La Calera, 200 m, *Trejo 1112* (US); Sindicatura Panuco, La Calera, *Gónzalez-Ortega 271* (MEXU); Mpio. Mazatlán, *Gónzalez-Ortega 7393* (US).

Philodendron dwyeri Croat, sp. nov. TYPE: Belize. Cayo: Macal (Macaw) River, Guacamallo Bridge, 16°52′N, 89°05′W, *Dwyer & Liesner 12334* (holotype, MO–2179389). Figure 155.

Planta epiphytica aut epilithica; succus albus; internodia longior quam lata, ca. 2 cm diam.; cataphylla probabiliter decidua; petiolus teres, 36.5 cm longus, 4 mm diam., leniter longior quam laminae; lamina ovata, 33 cm longa, 21 cm lata, in sicco cana-viridis supra, flaviviridis infra; sinus 7–8 cm profundus; inflorescentia 1; pedunculus 7 cm longus, 5 mm diam.; spatha 9.5 cm longa, omnino viridis, in sicco intus rubrobrunnea; pistilla 7–8-locularia; loculi 1-ovulati.

Epiphytic or epilithic; sap white; internodes slightly longer than broad, ca. 2 cm diam., semiglossy, epidermis light brown, drying conspicuously wrinkled and folded into sharp, irregular ridges; roots 3–4 mm diam., drying reddish brown with prominent ridges, semiglossy, with thin broad scales; cataphylls not seen, probably deciduous; **petioles** 36.5 cm long, 4 mm diam., terete; **blades** ovate, acute at apex (the acumen ± inrolled, 5 mm long), cordate at base, 33 cm long, 21 cm wide (1.5 times longer than wide), (0.9 times the petiole length), slightly shorter petioles, margins sinuate, upper surface drying gray-green, lower surface paler, drying yellow-green; anterior lobe 24.6 cm long, 21 cm wide (1.2 times longer than wide); posterior lobes 9 cm long, 9.5 cm wide, rounded, directed toward base; sinus 7–8 cm deep; midrib convex and concolorous above, convex and paler, drying yellowish, closely fissured and minutely warty below; basal veins 3 per side, with 1 free to base, 1 coalesced, second and third veins coalesced 1.9 cm; posterior rib not naked; primary lateral veins 5 per side, departing midrib at a 50–60(75)° angle; minor veins moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 7 cm long, 5 mm diam.; **spathe** 9.5 cm long (1.3 times longer than peduncle), visibly constricted above the tube, elliptic and to 5.5 cm wide when flattened, green throughout, green, drying reddish brown within; spathe tube ca. 4 cm long; **spadix** sessile; 7.2 cm long, broadest ± uniform throughout; pistillate portion cylindrical, 1.3 cm long, 1 cm diam.; staminate portion 6 cm long; fertile staminate portion cylindrical, 1 cm diam., broader than the pistillate portion, sterile staminate portion not detectable; pistils 1.1 mm long, 0.6 mm diam.; ovary 7–8-locular, 0.6 mm diam., with basal placentation; ovules 1 per

locule, 0.1 mm long, ± equal in length to funicle, style 0.6–0.8 mm diam., similar to style type D; style apex ± flat, with style boss; stigma subdiscoid, unlobed, 0.7–1.1 mm diam., 0.1 mm high, covering interior faces of stylar funnel; the androecium truncate, margins 4–6-sided; thecae oblong, very elongated, 0.2 mm wide.

Flowering in *Philodendron dwyeri* is documented by a single post-anthesis collection from January, early in the dry season.

Philodendron dwyeri is endemic to Belize, known only from the type collection in Cayo District of Belize at the Macal (Macaw) River near the Guacamallo Bridge at less than 500 m elevation.

Philodendron dwyeri is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* This species is characterized by having internodes longer than broad; white sap; terete petioles (slightly longer than blades); ovate blades drying gray-green above and much paler gray-green below with a very narrow sinus; solitary inflorescences with a green spathe; and ovaries with seven to eight locules and one ovule per locule.

Philodendron dwyeri is probably most easily confused with *P. breedlovei* from adjacent Chiapas, which is also a vine with blades of similar size and shape. That species differs, however, in having blades that dry dark yellow-brown with a more or less V-shaped sinus and ovaries with about 20 ovules per locule.

Additional specimen examined. BELIZE. **Cayo**: S of Guacamallo Bridge, *Whitefoord 2837A* (BM).

Philodendron edenudatum Croat, sp. nov. TYPE: Panama. Veraguas: along road from Santa Fe to Río Calovébora, vic. of Alto Piedra, on Atlantic slope, 0.6 mi. N of Escuela Agrícola Alto Piedra (now Escuela Primer Agrícola Alto Piedra), 735 m, 4 Apr. 1976, *Croat & Folsom 33988* (holotype, MO–2389069; isotypes, B, COL, CR, F, K, NY, US). Figures 156, 161–164.

Planta hemiepiphytica aut epiphytica; internodia 2.5–7.5 cm longa, 2–5 cm diam., viridia vel cana, in sicco pallide flavibrunnea; cataphylla 20–31 cm longa, acute 2-costata, decidua; petiolus subtere aut obtuse D-formatus, 34–41 cm longus, 1–1.5 cm diam., virens, guttatus purpureus; lamina ovata vel anguste ovata, cordata basi, 34–63 cm longa, 17–33 cm lata; costa postica haud nuda; inflorescentia 1; pedunculus 7–9 mm longus, 9–12 mm diam; spatha 10–13.5 cm longa; lamina spathae extus viridiflava, intus pallide viridi; tubo spathae extus atriviolaceopurpureo, intus atrimarronino; pistilla 7-locularia; loculi (3)4-ovulati.

Hemiepiphytic to epiphytic; appressed-climbing, leaf scars inconspicuous, 2 cm long, 2–2.5 cm wide; internodes moderately smooth and glossy, loosely and irregularly ribbed and grooved, 2.5–7.5 cm long, 2–5 cm diam., green to gray, soon brownish and ± densely transversed-fissured to scurfy and glossy to semiglossy, drying pale yellowish brown; epidermis flaking; roots 1–few per node, reddish brown; cataphylls 20–31 cm long, D-shaped to sharply 2-ribbed, green, spotted with purple, persisting intact at upper nodes, eventually deciduous; **petioles** 34–41 cm long, 1–1.5 cm diam., subterete to obtusely flattened or obtusely D-shaped adaxially, especially toward apex, medium to dark green, surface densely pale lineate, purple-spotted; sheathing up to ¾ its length; **blades** ovate to narrowly ovate, subcoriaceous, semiglossy, moderately bicolorous, abruptly acuminate at apex, cordate to subcordate at base, 34–63 cm long, 17–33 cm wide (1.8–2.2 times longer than wide), longer than petiole, upper surface drying gray to gray-brown, lower surface drying yellow-brown; anterior lobe 29–51 cm long, margins convex; posterior lobes 6–17 cm long, 6–13 cm wide, directed downward; sinus arcuate to V-shaped or rarely parabolic, (4)6–12 cm deep; midrib flat to concave, paler than surface above, convex to narrowly rounded, maroon-spotted and darker than surface, drying paler than surface below; basal veins 3–4 per side, second and higher (or sometimes only third and fourth) coalesced 0.5–4.5 cm; posterior rib not at all naked; primary lateral veins 5–6 per side, departing midrib at a 60–75° angle, weakly curved to gradually curved downward just before reaching the midrib, weakly sunken and paler above, convex and darker below; minor veins moderately distinct to ± obscure, arising from both the midrib and primary lateral veins, drying minutely undulate. INFLORESCENCES 1 per axil; peduncle 7–9 mm long, 9–12 mm diam., ± terete, light green, sometimes faintly tinged reddish medially on one side, clearly demarcated from spathe; **spathe** semiglossy, 10–13.5 cm long, 2–2.5 cm diam. midway, weakly constricted above the tube, oblong-ellipsoid, abruptly acuminate at apex (the acumen ca. 8 mm long); spathe blade greenish yellow outside, pale green, faintly striate inside, resin droplets forming on blade surface within; spathe tube 5 cm long, dark violet-purple with thin greenish margin (ca. 5 mm wide) and along a narrow band adaxially, faintly pale striate-speckled to faintly pale lineate outside, dark maroon inside; **spadix** sessile; gradually tapered to a blunt apex, 7.3–11.5 cm long; pistillate portion greenish, 4 cm long in front, 3.2 cm long in back, 1.2 cm diam.; staminate portion 7.3 cm long; fertile staminate portion 1.4 cm diam. at base, 1.1 cm diam. at middle, 8 mm diam. ca. 1 cm from

apex, broadest at the base; sterile staminate portion 1.4 cm diam.; pistils 2.3 mm long; ovary 7-locular, 1.7 mm diam., with sub-basal placentation; ovules 3(4) per locule, contained within gelatinous matrix (no true envelope), 0.5 mm long; funicle 0.3 mm long (can be pulled free to base), style 1 mm diam., similar to style type B; style apex flat; stigma lobed, 1 mm diam., 0.2 mm high, covering apical depressions (forming a ring without papillae in the center of the apex), depressed medially; the androecium truncate, prismatic, irregularly 4–6-sided, mostly 4–5-sided, 0.9–1.2 mm long; sterile staminate flowers irregularly 4–5-sided, prismatic, 1.3–1.8 mm long.

Flowering in *Philodendron edenudatum* possibly occurs in the dry season, based on a single, post-anthesis collection made in April.

Philodendron edenudatum is endemic to Panama, known in *Premontane rain forest* life zones at 110 to 1150 m elevation. It perhaps occurs in the adjacent Chocó of Colombia.

Philodendron edenudatum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is characterized by its slightly elongate internodes; sharply 2-ribbed cataphylls; somewhat D-shaped, usually purple-spotted petioles shorter than the blades; and ovate leaf blades with maroon-spotted midribs and posterior ribs which are never naked (hence the epithet "edenudatum," meaning not naked). Also characteristic are the solitary greenish inflorescences with the spathe tube dark purple-violet inside.

Philodendron edenudatum was first collected in 1979 at Alto de Piedra in Veraguas and more recently on Cerro Pirre in the Darién.

The species appears closest to *P. grayumii* and is perhaps only subspecifically distinct from that species. The latter differs in having more regularly and conspicuously ridged dried stems with a glossy, brownish yellow epidermis; petioles always longer than the blades (1.09–1.44 times longer); usually larger, more broadly ovate leaf blades (1.2–1.5 times longer than wide) with secretory ducts easily visible on the lower surface; and much larger inflorescences with ovaries having axile placentation (vs. sub-basal in *P. edenudatum*).

Additional specimens examined. PANAMA. **Darién**: Parque National Cerro Pirre, W side, 550–760 m, 7°57′N, 77°46′W, *Croat 68891* (CM, MO, PMA, US); *68901* (CM, MO); *68903* (MO); vic. of field station along Río Perisenico, 17 km N of El Real, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77087* (MO, NY, US); 100 m, *77185* (CAS, CM, MEXU, MO, VEN); vic. Cerro Pirre, trail to Rancho Frío on slopes of Cerro Pirre, 200–450 m, 7°58′N, 77°43′W, *Croat & Zhu 77157* (AAU, CM, MO, US); Serranía de Pirre above Cana Gold Mine, Río Cana–Río Escucha Ruido, 600–1000 m, *Croat 37741* (MO). **Veraguas**: Santa Fe–Río Calovébora, 1.7 mi. past Escuela Agrícola Alto Piedra, 570 m, 8°38′N, 81°08′W, *Croat & Zhu 76861* (CM, MO); trail to top of Cerro Tute, 1050–1150 m, *Croat 48904* (MO); *48906* (MO, US).

Philodendron ferrugineum Croat, sp. nov. TYPE: Panama. Panamá: along El Llano–Cartí road, 8.3 mi. above Inter-American Hwy., 380 m, 17 July 1987, *Croat 67400* (holotype, MO–3582221–22; isotypes, AAU, B, CM, COL, CR, F, K, L, MEXU, PMA, US). Figures 165–168, 173, 174, 185.

Planta hemiepiphytica; internodia brevia, 3–5 mm diam.; cataphylla (15)26–48 cm longa, incostata aut obtuse 2-costata prope apicem; petiolus teres aut semiteres, 41–67 cm longus, 1–1.3 cm diam., circa tam longus quam lamina; lamina anguste ovata, manifeste cordata basi, (38)56–85(102) cm longa, 17–56(62) cm lata, in sicco rubribrunnea; venis minoribus obscuris, arcte dispositis, ut videtur intermittentibus; inflorescentia 4–6; pedunculus 2.5–11 cm longus, 1–2 cm diam.; spatha 16–23 cm longa; lamina spathae extus pallide viridi, intus albida; tubo spathae viridi, extus dense maculato violaceo-purpureo, intus purpureo-violaceo vel pallide marronino; pistilla 8–10-locularia; loculi 4–7-ovulati; baccae aurantiacae.

Hemiepiphytic; stem appressed-climbing, pale to dark green, soon brown, to 1 m long, leaf scars conspicuous, 2.5–3 cm long, 2–5 cm wide; internodes semiglossy, short on adult plants, 3–5 cm diam., sometimes longer than broad, pale to dark green, becoming gray, finally brown, somewhat scurfy, sometimes transversly fissured; roots dark brown, to ca. 30 cm long, 1–2 cm diam., drying reddish brown; cataphylls (15)26–48 cm long, unribbed, except bluntly or sharply 2-ribbed near apex, green, blotched with purple-violet, to paler green or whitish to densely dark green speckled, maroon spotted or tinged, sulcate between ribs, drying reddish brown, deciduous, persisting weakly at upper nodes, rounded at apex margins clear to hyaline. LEAVES spreading-pendent, scattered evenly along stem, clustered at or near stem apex; **petioles** 41–67 cm long, 1–1.3 cm diam. (about as long as the blade), erect-spreading, terete or subterete, dark green, firm, weakly and obscurely sulcate adaxially, often obtusely flattened and obtusely ribbed toward apex, to bluntly and broadly sulcate near base adaxially, surface weakly glossy to matte, weakly and densely light green-lineate or striate, purplish red ring around apex; sheathing to 6 cm long; geniculum thicker than petiole, 2.5–3.5 cm long, slightly paler than petiole; **blades** pendent, narrowly ovate, moderately coriaceous, bicolorous, gradually to strongly acuminate at apex (the acumen tightly inrolled), cordate at base, (38)56–

85(102) cm long, 17–56(62) cm wide (1.3–2.3 times longer than wide), (0.8–1.3 times longer than petiole), about equal in length to petiole, broadest somewhat above point of petiole attachment, or at lower one-third, margins hyaline, weakly to strongly undulate; upper surface dark to medium green, drying coriaceous, reddish brown, semiglossy to glossy, weakly arched along midrib; lower surface very weakly glossy to matte, much paler, drying with minute uninterrupted ridges; anterior lobe 42–70 cm long, 9–22.2 cm wide ((7.5)12–27 times longer than posterior lobes), margins broadly convex; posterior lobes 14–27 cm long, directed downward or inward, sometimes overlapping, obtuse to rounded; sinus strongly spathulate to hippocrepiform; midrib flat to weakly convex, paler than surface above, convex to narrowly rounded, lineate, sometimes maroon-spotted, dark green, paler than surface, drying dark yellowish brown below; basal veins 2–3–5 per side, with 1(2) free to base, 2–5 coalesced 2–4.5 cm, convex and paler than surface above, bluntly acute to convex below; posterior rib not naked, straight to weakly curved; primary lateral veins 5–8 per side, departing midrib at a 45–70° angle, ± straight, slightly curved toward apex, pale green to whitish, usually obtusely sunken, sometimes to weakly and bluntly raised above, convex and darker than surface below; interprimary veins weakly visible to inconspicuous above and below; secondary veins drying inconspicuous; minor veins moderately obscure, close and apparently intermittent, giving veins a bumpy look, arising from both the midrib and primary lateral veins. INFLORESCENCES semi-erect to erect, 4–6 per axil; peduncle 2.5–11 cm long, 1–2 cm diam., whitish at base; **spathe** coriaceous, 16–23 cm long (1.6–4.2 times longer than peduncle), slightly constricted above the tube, acuminate (the acumen inrolled), dark green outside; spathe blade with lateral margins rolled back, sometimes pale green outside, whitish inside; spathe tube green, heavily spotted with purple-violet outside, 6–8(12) cm long, purple-violet to light maroon, at least the lower ⅗, otherwise greenish white inside; **spadix** sessile; clavate, weakly protruding forward at anthesis, 12–20 cm long, broadest above the middle, constricted weakly above sterile staminate portion; pistillate portion pale green to yellow, cylindrical or tapered toward the apex to narrowly ellipsoid, 3.7–6.5(8) cm long, 1.3–1.5 cm diam. at apex, 1.6 cm diam. at middle, 1.1–1.8 cm wide at base; staminate portion 8.6–16 cm long; fertile staminate portion white to yellowish, ± ellipsoid to clavate, 1.1–1.5 cm diam. at base, 1.3–1.9 cm diam. at middle, 1.1–1.5 cm diam. ca. 1 cm from apex, broadest at the middle or at the base, broader than the pistillate portion, broader than the sterile portion; sterile staminate portion narrower than the pistillate portion, white, 1.5 cm diam.; pistils 2–3.4 mm long, (0.7–0.8)1.6–2 mm diam.; ovary 8–10-locular, 1.6 mm diam., with sub-basal (axile) placentation; ovules 4–7 per locule, 1-seriate, 0.4–0.5 mm long, longer than (or equal in length to) funicle; funicle adnate to lower part of axile wall; style 1.1–1.6 mm diam., similar to style type D; style apex flat, with raised annulus; style boss broad; stigma button-like with medial depression, 1.3 mm diam., 0.2–0.5 mm high, covering entire style apex except (including annulus) in center, medially and shallowly depressed; the androecium truncate, margins 4–6-sided, irregularly scalloped or lobed on at least one margin; thecae oblong, 0.4–0.5 mm wide, contiguous; sterile staminate flowers rounded or blunt, 2.2–2.5(4) mm long, (1.9)2.2–3.2 mm wide, 2.2–2.5(4) mm long. INFRUCTESCENCE erect to semi-erect; berries turning orange, obovoid-ellipsoid, apex blunt, 0.8–1.2 mm long, 0.5 mm diam.; mesocarp pale yellow to orange; seeds 3–7 per locule, pale and striate or brown and smooth, strongly sulcate, 1–1.5 mm long, 0.5–0.6 mm diam., enclosed in a translucent envelope. JUVENILE blades narrowly ovate, rounded at base, gradually acuminate at apex, ± shorter than petiole.

Flowering in *Philodendron ferrugineum* is recorded by only one collection in August, although post-anthesis collections range from May through September, indicating that the species probably flowers in the rainy season.

Philodendron ferrugineum is currently known only from Panama, from 0 to 770 m elevation in *Tropical wet forest* and *Premontane wet forest* life zones.

Philodendron ferrugineum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is distinguished by its short internodes; unribbed, deciduous cataphylls; terete to subterete petioles about equaling the blades; and large, thick, cordate blades drying reddish brown with the minor veins obscure, close, and apparently intermittent with a bumpy look. Also characteristic are the 4–6 inflorescences per axil with the spathe tube green outside and maroon inside.

Philodendron ferrugineum can be confused with *P. llanense* Croat, with which it occurs in both Bocas del Toro and on the El Llano Cartí Road and Cerro Jefe in Panamá Province and which has similar blades. The latter species differs in having cataphylls becoming fibrous and blades drying greenish brown to somewhat blackened, never

conspicuously reddish brown. *Philodendron ferrugineum* has also been confused with *P. grayumii*. See the discussion of that species for differences.

A similar, apparently undescribed species from Colombia resembles *P. ferrugineum* in its large ovate, thick blades (especially in living condition) and in having three to four inflorescences per axil. Examples include *Croat 56246, 56708,* and *Monsalve 911* from Bajo Calima near Buenaventura in Valle Province. These differ, however, in drying grayish brown above and yellowish brown beneath and in having interrupted secretory ducts between the minor veins. In addition, they do not have the undulated and puckered minor veins on drying that are so characteristic of specimens of *P. ferrugineum.*

A noteworthy collection is *McPherson 11479,* which is somewhat intermediate between *P. ferrugineum* and *P. grayumii.* That collection has blades that dry more reddish brown and have a bumpy surface but also secretory ducts. It may prove to be a new species.

Additional specimens examined. PANAMA. **Bocas del Toro**: Chiriquí Lagoon, on Cayo Agua, 5 m, 9°10′N, 82°W, *McPherson 11479* (AAU, MO); Escudo de Veraguas Island, 5 m, 9°05′N, 81°35′W, *McPherson 11410* (MO, PMA). **Colón**: Santa Rita Ridge Road, along trail to Río Indio, 10.6 km from Transisthmian Highway, 380 m, *Croat 34349* (MO); along route between Sabanitas and Portobello, 3.9 mi. from highway, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75155* (AAU, BR, CM, L, MO, PMA); Río Agustín, Río Guanche, ca. 0 m, 9°30′N, 79°40′W, *Churchill et al. 6018* (MO); Río Iguanita, ca. 3 km above bridge on Portobelo road, <100 m, 9°27′N, 79°40′W, *Croat 49749* (MO). **Panamá**: El Llano–Cartí Road, *Croat 33145A* (MO); Km 7–12 km, 360–400 m, *25098* (MO); 5–6 mi. N of highway, 350–375 m, *34787* (MO); Mile 3.4, 1000 ft., *49098* (MO); Mile 4, *33732* (CAS, F, MO, NY); Km 7–12, 360–400 m, *25173* (MO); Km ca. 17, 400 m, 9°15′N, 78°50′W, *Knapp 1376* (MEXU, MO); Cerro Jefe region, 9°15′N, 79°30′W, *Croat & Zhu 76216* (CM, MO); 21 km above Pan-American Highway, 600 m, *Croat 35886* (MO); 750–800 m, 9°14′N, 79°22′W, *Croat 67092A* (CM, MO, PMA); 4.6 km beyond peak on road to Altos de Pacora, 26.3 km from Inter-American Highway, 600 m, *Croat 35923* (MO); at Altos de Pacora, 750 m, 9°15′N, 79°29′W, *Croat & Zhu 76607* (CM, MO); 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76612* (CR, MO, NY). **San Blas**: Nusagandi, along El Llano–Cartí Rd., 0.7 mi. beyond Cuna Headquarters, located 10.9 mi. N of Pan-American Highway, 450 m, 9°18′N, 79°59′W, *Croat 75116* (CM, MO, PMA, TEX); 300–400 m, 9°20′N, 79°W, *Hamilton & Stockwell 1073* (MO); 1–2 mi. N of Nusagandi on road to Cartí, 250–275 m, 9°20′N, 79°W, *Croat & Zhu 76577,* (CAS, L, MO, PMA, US); *76580* (CM, MO, SEL, WIS); Mile 10.1, 300 m, 9°20′N, 79°W, *Croat & Zhu 77029* (COL, CR, MEXU, MO); *77030* (MO, PMA).

Philodendron findens Croat & Grayum, sp. nov. TYPE: Panama. Chiriquí: Fortuna Dam area, Fortuna–Chiriquí Grande, 1.8 mi. NW of center of dam, 1080 m, 8°45′N, 82°18′W, 27 June 1994, *Croat & Zhu 76502* (holotype, MO–4619581–84; isotypes, B, COL, CR, F, K, NY, PMA, US, VEN). Figures 7, 34, 169–171, 175, 177, 178.

Planta plerumque hemiepiphytica, varius terrestris; internodia 4–9 cm longa, 2–4 cm diam.; cataphylla usque 35 cm longa, acute 2-costata, persistentia semi-intacta nodis superioribus, fibrosentia, demum decidua; petiolus D-formatus, (25)43–119 cm longus, 0.6–35(45) cm diam., cum ala marginali tenui, erecta; lamina ovato-cordata, (25)40–76 cm longa, (20.5)28–70 cm diam., findens inter nervos laterales I sic videtur fere pinnata, in sicco denigrata; inflorescentia 2; pedunculus 4–12(15) cm longus, 0.3–1.4 cm diam.; spatha 13–22.8 cm longa; lamina spathae extus virenti vel pallide viridi; intus viridialba; tubo spathae extus viridi, intus rubro; pistilla 5–6-locularia; loculi 15–20(22)-ovulati.

Usually hemiepiphytic, rarely terrestrial on steep banks; stem appressed-climbing, medium green, glossy, sap watery, spicy-scented, leaf scars conspicuous, 3.5–4 cm long, 5 cm wide; internodes short, thick, semiglossy, 4–9 cm long, 2–4 cm diam., longer than broad, dark olive-green, epidermis cracking, yellowish, fissured longitudinally and transversely; roots moderately few per node, drying dark brown, semiglossy, acutely ridged; cataphylls thin, fleshy, somewhat spongy, to 35 cm long, sharply 2-ribbed (ribs 2–3 mm high), D-shaped, thicker than broad, medium green, light or pale yellow-green toward margins, semiglossy, broadly sulcate abaxially, persisting semi-intact at upper nodes, becoming fibrous and eventually deciduous, blunt to acute at apex, margins weakly raised adaxially; **petioles** (25)43–119 cm long, 0.6–35(45) cm diam., sharply D-shaped, with a thin, erect marginal wing, the wing undulate toward apex, surface densely light striate near base; **blades** large ovate-cordate, subcoriaceous, strongly bicolorous, short acuminate at apex, cordate at base, (25)40–76 cm long, (20.5)28–70 cm wide (1.1–1.5 times longer than wide), (0.6–1.1 times longer than petiole), margins usually promptly splitting into segments by dividing between the primary lateral veins, making blades appear almost pinnate, upper surface dark green, semiglossy, drying blackened to dark reddish brown, nearly matte, lower surface semiglossy to matte, paler; anterior lobe 18–57.5 cm long, 15.5–55(79) cm wide (2.2–3.2 times longer than posterior lobes); posterior lobes (7.2)11.5–32 cm long, 8.6–28(37.5) cm wide, obtuse to rounded; sinus ± parabolic; midrib weakly to deeply sunken, paler than surface above, con-

vex, weakly striate, slightly paler than surface below; basal veins 5–12 per side, with 0–1(2–3) free to base, in part coalesced 5–10 cm; posterior rib naked for 1–7 cm; primary lateral veins 5–7 per side, departing midrib at a 40–50° angle, deeply sunken and paler than surface above, convex, usually concolorous below; interprimary veins visible, few near apex above and below; tertiary veins visible, darker than surface below; minor veins weakly raised and darker than surface, arising from both the midrib and primary lateral veins; secretory canals obscurely visible. INFLORESCENCES erect, 2 per axil; peduncle 4–12(15) cm long, 0.3–1.4 cm diam., pale to medium green, prominently, densely white-streaked; **spathe** 13–22.8 cm long (1.4–2.4 times longer than peduncle), constricted midway slightly above the tube; spathe blade medium to pale green outside, greenish white inside; spathe tube oblong-ellipsoid, green, densely and minutely lineate-speckled outside, 7–9 cm long, red (B & K red-purple 4/10, 2/10) inside; **spadix** sessile, tapered, 13–23 cm long, broadest just below the middle; pistillate portion gray-white, tapered toward the apex, slightly curved, 4–8.5 cm long, 1.4–2.1 cm diam. at apex, 1.6 cm diam. at middle, 1.9 cm wide at base; staminate portion 14.3–17.5 cm long; fertile staminate portion creamy white, tapered, 1.8–2 cm diam. at base, 1.3 cm diam. at middle, 9 mm diam. ca. 1 cm from apex, broadest at base, narrower than the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, 1.6 cm diam.; pistils (3)7.7–8.4 mm long, 2–2.5 mm diam.; ovary 5–6-locular, locules (1.6)5.8–6.1 mm long, with axile placentation; ovules 15–20(22) per locule, 2-seriate, 0.3–0.5 mm long, longer than funicle, style similar to style type B; style apex rounded; stigma subdiscoid to discoid, ± lobed, 1.2–2 mm diam., 0.1–0.5 mm high, covering entire style apex; the androecium truncate, 4–6-sided; thecae oblong, 0.5 mm wide, contiguous; sterile staminate flowers blunt, 3.1 mm long, 1.2 mm wide. INFRUCTESCENCE 12 cm long, 3.7 cm diam., 19.5 cm long; stipe 4.5 cm diam.; berries irregularly quadrangular to bluntly 4–5-sided, with a kiwi-fruit scent, 3.5–4.2 mm diam.; seeds 1–2 per locule, ca. 17 per berry, somewhat flattened, 1.5–2.2 mm long, 0.3–0.4 mm diam., translucent and with fine striations. JUVENILE stems dark green to yellow-brown, semi-glossy to glossy, 2.4 cm long, 5 mm diam.; blades thin, entire. PRE-ADULT petioles broadly convex adaxially, the margins spreading winged, incurled, erect; blades moderately bicolorous.

Flowering in *Philodendron findens* occurs in May and July, but post-anthesis and immature fruiting collections from March through November (except October) suggest a broader flowering period, with plants flowering earlier in the dry season or much later in the rainy season.

Philodendron findens ranges from Costa Rica to Panama on the Atlantic slope, from near sea level to 1400 m elevation in mostly *Tropical wet forest* and *Premontane rain forest* but also in *Premontane wet forest*. It probably also occurs in Colombia.

Philodendron findens is a member of *P.* sect. *Philodendron* subsect. *Platypodium*. This species is characterized by its generally appressed-climbing habit and short, thick internodes with sharply two-ribbed cataphylls, which are finally fibrous and persistent; D-shaped petioles with marginal wings adaxially; and especially by its usually black-drying, large, ovate-cordate, leaf blades, which promptly shred into segments, making the blade appear almost pinnate (hence the name "findens," meaning "tearing or splitting"). Also characteristic are the paired, green inflorescences with the spathe tube red within.

Philodendron findens can be confused with *P. pterotum*, which has similarly shaped blades and D-shaped petioles with narrowly winged margins. That species differs, however, in having blades drying yellow-green, and major veins drying paler than the surface below (in contrast to blackened and darker than the surface in *P. findens*) and do not rip into segments, and also by occurring more commonly in *Tropical moist forest* and at elevations of usually less than 400 m. In addition, the spathe tube in *P. pterotum* is purplish on the outside, vs. solid green (sometimes reddish) for *P. findens*.

Cuatrecasas 14948, from Valle Department along Río Digua at Piedra de Moler at 900–1180 m, is apparently this species. It differs in no significant way, but there are no field notes and the petiole is improperly preserved so its cross-sectional shape cannot be confirmed.

Additional specimens examined. COSTA RICA. **Alajuela**: ca. 7.5 km N of bridge over Río Balsa, 700–800 m, 10°10–15′N, 84°30–35′W, *Stevens 13892* (MO); ca. 5.7 km N of bridge over Quebrada Volio, 1100–1150 m, 10°08′N, 84°29′W, *Stevens 14115* (MO); San Ramón Forest Reserve, ca. 10 km W of Laguitos, along Río San Lorencito, 850–1100 m, 10°18′N, 84°34′W, *Hammel et al. 15283* (MO); ca. 1.3 mi. N of Angeles Norte, 1200 m, *Croat 46876* (MEXU, MO); 800–1000 m, *Nilsson 458* (CR); Reserva Biológica Monteverde, 950 m, 10°18′N, 84°45′W, *Bello & Méndez 2667* (MO); *2668* (CR); 820 m, 10°19′N, 84°43′W, *Bello & Eyol 2682* (INB, MO). **Cartago**: Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36627* (MO); Río Navarro, El Muñeco, 1400–1500 m, *Standley & Torres 51355* (US). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35796* (MO); *35813* (MO); 4 mi. N of Vara Blanca, 1350

m, *Croat 35606* (MO); Río Frío de Sarapiquí, Río Sucio–Finca Zona Ocho, 110 m, 10°18′N, 83°52.5′W, *Grayum & Hammel 5565* (CR, L, MO); Río Frío, W of Finca Zona Nueve, ca. 110 m, 10°18′N, 83°53′W, *Grayum 3561* (K, M, MO, RSA). **Limón**: Fila Lleskila Talamanca, 1160 m, *Gómez et al. 23061* (CM, K, MO). **San José**: Braulio Carrillo National Park, 600-700 m, *Croat 78751* (CM, CR, INB, M, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 470 m, 8°50′N, 82°15′W, *McPherson 11646* (MO); ca. 0 m, 8°55′N, 82°09′W, *Croat 66811* (MO); Almirante–Ojo de Agua, 3–6 km W of Almirante, 30–200 m, *Croat 38218* (BR, CAS, F, K, MO, PMA, US); 2.8 mi. N of Divide, 850–950 m, 8°45′N, 82°15′W, *McPherson 9674* (MO, NY). **Chiriquí**: Gualaca–Chiriquí Grande, 1.4 mi. W of Centro de Operaciones, trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67919* (B, F, K, M, MO); *Croat & Zhu 76293B* (MO); Río Chiriquí, near La Sierpe, ca. 0.5 km N of river, IRHE Fortuna Hydroelectric Project, 1000–1100 m, 8°46′N, 82°12′W, *Knapp 5052* (MO). **Coclé**: El Valle de Antón region, at La Mesa, 860–900 m, *Croat 37410* (MO); 775 m, 8°36′N, 80°07′W, *74795* (MO); 800–900 m, 8°38′N, 80°09′W, *67153* (MO); *Luteyn & Kennedy 1616* (MO); El Copé region, N of El Copé, 1200–1300 m, *Sytsma & Andersson 4622* (MO). **Colón**: 10 mi. SW of Portobelo, 2–4 mi. from coast, 10–200 m, *Liesner 1115* (F, MO, NY, US); Río Guanche, ca. 2 km E of bridge on main Puerto Pilón–Portobelo Road, 100 m, ca. 9°30′N, 79°39′W, *Croat 75175* (B, CAS, COL, F, K, MO, NY, PMA, US). **Darién**: along headwater of Río Tuquesa, ca. 2 km air distance from Continental Divide, Tyler Kittredge gold mine, *Croat 27148* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río San Luis, beyond Escuela Agrícola Alto de Piedra, 5.9 mi. N of school, 480 m, 8°33′N, 81°08′W, *Croat 66937* (MO, PMA, US); trail up Cerro Tute, 1050–1150 m, *Croat 48899* (CM, MO); Escuela Agrícola Alto de Piedra–Río San Luis, vic. of Santa Fe, along Río Primero Brazo, on Atlantic Coast, 490 m, 8°33′N, 81°08′W, *Croat 66879A* (MO); Escuela Agrícola Alto Piedra–Calovébora, 15.6 km NW of Santa Fe, along trail to Santa Fe, E of Río Dos Bocas, 450–550 m, *Croat 27653* (MO); beyond Tres Bravos River, 11 km beyond Santa Fe, 650 m, *Croat 25625* (MO).

COLOMBIA. **Valle**: Cordillera Occidental, Río Digua, Piedra de Moler, 900–1180 m, *Cuatrecasas 14948* (F).

Philodendron folsomii Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, 9 km N of El Copé, N of Continental Divide along path to W, ca. 800 m, 8°40′N, 80°37′W, 24 Jan. 1989, *McPherson 13619* (holotype, MO 3693168; isotypes, B, K, PMA, US). Figures 172, 176.

Planta epiphytica; internodia brevia, 1–1.5 cm longa, 8–20 mm diam.; cataphylla 11–16 cm longa, acute 2-costata, decidua; petiolus subteres, obtuse sulcatus, 12–17 cm longus; lamina oblongo-lanceolata, 28–33 cm longa, 5–7 cm lata, rotundata aut truncata basi; inflorescentia 1–2; pedunculus 10–11.5 cm longus, 2–5 mm diam.; spatha 10–12 cm longa, extus alba; pistilla 6–7-locularia; loculi 1-ovulati.

Epiphytic; stem scandent; internodes short, 1–1.5 cm long, 8–20 mm diam., about as long as broad; cataphylls 11–16 cm long, sharply 2-ribbed, green, deciduous; roots not seen; **petioles** 12–17 cm long, 3–5 mm diam., subterete, obtusely sulcate; **blades** oblong-lanceolate, narrowly acuminate at apex, obtuse to almost rounded and decurrent, sometimes nearly truncate at base, 28–33 cm long, 5–7 cm wide (4.6–5.2 times longer than wide), (1.8–2.3 times longer than petiole), upper surface drying gray-green to brownish green; lower surface paler, drying yellowish green; midrib sunken above, convex, drying paler than surface below; basal veins 1–2, free to base; primary lateral veins 8–10 per side, departing midrib at a 35° angle, arcuate to the margins, distinct above; minor veins arising from the midrib only. INFLORESCENCES 1–2 per axil; peduncle 10–11.5 cm long, 2–5 mm diam.; **spathe** 10–12 cm long (about as long as the peduncle), white throughout outside; spathe tube 5.5 cm long, 2.5 mm diam.; **spadix** short stipitate; 7–8 cm long; pistillate portion 3–4.1 cm long, 6–7 mm diam.; staminate portion 3.8–4 cm long; sterile staminate portion whitish; pistils 0.8 mm long, 0.6 mm diam.; ovary 6–7-locular, locules 0.6 mm long, 0.3 mm diam., ovule sac 0.6 mm long, with subbasal placentation; ovules 1 per locule, contained within gelatinous transparent matrix (no true envelope), 0.2–0.35 mm long, as long as funicle; funicle 0.2–0.3 mm long (can be pulled free to base), with glands at base, style similar to style type B; style apex flat; stigma subdiscoid, unlobed, ± truncate, 0.9 mm diam., 0.3 mm high, covering almost entire style apex; the androecium truncate, prismatic, margins irregularly 5–6-sided, 0.6–0.8 mm long.

Flowering phenology in *Philodendron folsomii* is uncertain because few collections exist. Flowering collections are known from January and April, both within the dry season but in an area that is not markedly seasonal.

Philodendron folsomii is endemic to Panama, known only from the type locality in Coclé Department, at 700 to 800 m elevation in *Premontane rain forest.*

Philodendron folsomii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is characterized by internodes about as long as broad; sharply two-ribbed, deciduous cataphylls; oblong, narrowly acuminate, oblong-lanceolate, green-drying blades with obtuse-attenuate bases; and solitary, long, slender-pedunculate inflorescences with white spathes.

Philodendron folsomii is most easily confused with *P. sphalerum* Schott from the Guianas and eastern Venezuela, which has similar leaves. The latter species differs in having smaller, generally

more numerous (up to four) inflorescences per axil with more slender peduncles (drying scarcely 2 mm diam. vs. 4 mm or more in *P. folsomii*) and spathes less than 7 cm long (vs. 10–13.5 cm long in *P. folsomii*).

Philodendron folsomii is also similar to *P. correae*, which has similarly shaped leaf blades that also sometimes dry green. The latter species differs in having generally longer internodes; petioles usually sheathed to near the apex; blades usually drying black and lacking conspicuous primary lateral veins; and spathes not so conspicuously constricted above the tube.

Additional specimen examined. PANAMA. **Coclé**: El Copé region, 700 m, *Folsom & Robinson 2447* (MO).

Philodendron fortunense Croat, sp. nov. TYPE: Panama. Chiriquí: Gualaca–Chiriquí Grande Road, vic. of Fortuna Dam, at junction of road to IRHE headquarters, 1200 m, 8°45′N, 82°18′W, 23 June 1987, *Croat 66714* (holotype, MO–3635169; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, EAP, F, GH, HUA, K, L, M, MEXU, NY, P, PMA, QCNE, RSA, S, SEL, TEX, US, VEN). Figures 179, 181–184.

Planta terrestris aut hemiepiphytica; internodia 3–6 cm longa, 4–7 cm diam.; cataphylla 18–32 cm longa, acute 2-costata, glauca, deciduа; petiolus plus minusve D-formatus, 49–70 cm longus, 1.2–2.5 cm diam., glaucus, marginibus manifeste alatus, alis undulatus; lamina ovato-cordata vel oblongato-ovata, cordata basi, 36–60 cm longa, 22–44 cm lata; inflorescentia 4; pedunculus 7.7–8 cm longus, 8 mm diam.; spatha 20–21 cm longa, omnino virens, tubo spathae marronino, intus suffuso marronino in laminam; pistilla 7–8-locularia; loculi 9–10-ovulati.

Terrestrial or hemiepiphytic; stem appressed-climbing, 2–3 m long, thick, leaf scars conspicuous, 1.2–1.7 cm long, 2–2.5 cm wide; internodes smooth, to weakly pruinose, 3–6 cm long, 4–7 cm diam., about as long as broad, green to olive-green, epidermis drying smooth, semiglossy, light yellow-brown (B & K yellow-red 9/10), cracking with age, fissured transversely, sometimes with minute cracks perpendicular to axis; roots few per node, elongate, to 4 mm diam., light brown, smooth, weakly glossy, the epidermis cracking free upon drying; cataphylls thick, 18–32 cm long, sharply 2-ribbed (ribs 4 mm high), pale green, glaucous, dark short-lineate, deciduous. LEAVES erect-spreading, clustered at or near stem apex; **petioles** 49–70 cm long, 1.2–2.5 cm diam., ± D-shaped, becoming flattened and much broader than thick toward apex, medium green, rounded to flattened abaxially, with adaxial margins prominently winged (to 3 mm diam.), undulate to broadly flattened, surface dark short-lineate, glaucous; **blades** ovate-cordate to oblong-ovate cordate, moderately coriaceous to subcoriaceous, gradually acuminate to abruptly acuminate at apex, cordate at base, 36–60 cm long, 22–44 cm wide (1.3–1.8 times longer than wide), (0.85–0.88 times the petiole length), broadest slightly above point of petiole attachment, margins moderately undulate, upper surface medium green, semiglossy, drying greenish yellow, lower surface medium to pale green, glaucous, matte, paler, drying greenish yellow; anterior lobe 28–44 cm long, 10–20 cm wide (0.9–1.3 times longer than wide), (1.8–2.9 times longer than posterior lobes), broadest at base; posterior lobes usually overlapping, 10–20 cm long, 10–20 cm wide, directed downward and slightly inward, obtuse to rounded; sinus oblong-triangular or closed, 10–19 cm deep; midrib flat to weakly raised, pale green, concolorous above, weakly raised, paler than surface below; basal veins 5–10 per side, 1–2 pairs free to base, the remainder mostly free, sometimes weakly coalesced 1–4 cm, drying weakly raised; posterior rib usually not present, naked and straight if present; primary lateral veins 7–11(15) per side, departing midrib at a 30–45° angle, straight or slightly arcuate to the margins, flat to sunken and drying darker than surface above, convex and darker than surface below; interprimary veins prominulous, weakly sunken to flat, concolorous above, flat and darker than surface below; lesser veins visible when dried; minor veins conspicuous, fine, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES 4 per axil; peduncle 7.7–8 cm long, 8 mm diam., medium green; **spathe** ± erect, 20–21 cm long (2.5–2.7 times longer than peduncle), medium green throughout, glaucous, ± acute at apex; spathe tube maroon, suffused maroon onto blade inside; **spadix** sessile; tapered, 20–21 cm long; pistillate portion tapered toward the apex, 5.2 cm long, 1.3 cm diam. at apex, 1.5 cm diam. at middle, 1.7 cm wide at base; staminate portion 14.7 cm long; fertile staminate portion tapered, 1.4 cm diam. at base, 1.3 cm diam. at middle, 1.1 cm diam. ca. 1 cm from apex, broadest at the base, narrower than the pistillate portion, narrower than the sterile portion; sterile staminate portion narrower than the pistillate portion, 1.4 cm diam.; pistils 4.5 mm long, 2.1–2.4 mm diam.; ovary 7–8-locular, locules 1.9 mm long, with sub-basal placentation; ovules 9–10 per locule, 0.4–0.5 mm long, slightly longer than funicle, style 2 mm long, 1.8 mm diam., similar to style type B; style apex flat; stigma subdiscoid, unlobed, 2 mm diam., 0.4 mm high, covering entire style apex; the androecium truncate, margins 4–6-sided; thecae oblong, 0.5 mm wide,

contiguous; sterile staminate flowers blunt, 3.2 mm long, 1.7 mm wide.

Flowering in *Philodendron fortunense* is known only from April, and immature fruits from June. This corresponds to the late dry season and early rainy season in most of Panama, though this species occurs in an area with little seasonality.

Philodendron fortunense is endemic to Panama, known only from Chiriquí Province in the Fortuna Dam region (hence the name), from 1100 to 1300 m in elevation in regions of *Premontane rain forest.*

Philodendron fortunense is a member of *P.* sect. *Philodendron* subsect. *Platypodium.* This species is recognized by its thick stems with short, smooth (when fresh), green internodes; sharply two-ribbed, glaucous, deciduous cataphylls; ovate-cordate blades with usually overlapping posterior lobes, and pale, glaucous lower surfaces; and especially by the glaucous, broadly flattened petioles with undulate-winged margins.

Philodendron fortunense, one of the showiest, most distinctive species in the Central American region, is not easily confused with any other species. Its greatest similarity is to *P. brenesii,* with which it may occur, but that species differs in having proportionately longer, more or less terete petioles, and one to two inflorescences per axil (vs. up to four inflorescences per axil in *P. fortunense*).

Additional specimens examined. PANAMA. **Chiriquí**: Fortuna Dam area, Gualaca–Chiriquí Grande, jct. of road to IRHE headquarters, 1200–1300 m, 8°45′N, 82°18′W, *Croat 66529* (CM, ENCB, HNMN, JAUM, MO, MY, QCA, RB, W); 9.6 mi. beyond Los Planes de Hornito, 1300 m, *Croat 48727* (AAU, COL, F, MO, OOM, QCNE); *48728A* (MO); 10.1 mi. NW of Los Planes de Hornito, 1300 m, 82°17′W, 8°45′N, *Croat 49814* (MO); *50000* (BR, CAS, CM, L, MO, QCA, SCZ, TEX); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60000* (B, CM, K, MO, NY, RSA, US); 8 mi. beyond Los Planes de Hornito, 1.4 mi. W of Centro de Operaciones, trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67921* (G, M, MO).

Philodendron fragrantissimum (Hook.) G. Don, in Sweet, Hort. Brit. ed. 3: 632. 1839. Figures 30, 186–191. *Caladium fragrantissimum* Hook., Bot. Mag. 61: t. 3314. 1834. TYPE: Guayana (specimen introduced by C. S. Parker in 1834 to Liverpool Botanical Garden) (holotype, K).

Philodendron latipes K. Koch & Augustin, in A. Braun et al., Append. Gen. Sp. Hort. Berol. 1854: 6. 1854–1855. TYPE: origin unknown (holotype, B destroyed); *Burchell 9452* (neotype, here designated, K).

Philodendron poeppigii Schott, Syn. Aroid. 84. 1860. TYPE: Brazil. Amazonas: (Ega) Tefé, *Poeppig s.n.* (holotype, B).

Philodendron brevilaminatum Schott, J. Bot. 2: 4. 1864. TYPE: Brazil. Bahia: Ilheos, *Archduke F. Maximilianius s.n.* (holotype, lost); Schott ic. 3592 (neotype, here designated).

Philodendron clementis C. Wright, in Griseb., Cat. Pl. Cub., 220. 1866. TYPE: Cuba. Near Retiro, *Wright 3212* (lectotype, here designated, K).

Philodendron demerarae Gleason, Bull. Torrey Bot. Club 56: 11. 1929. TYPE: Guyana. SE of Lamaha stop-off, 27 Nov. 1919, *Hitchcock 16987* (holotype, NY).

Philodendron accrescens N. W. Simmonds, Kew Bull. 1951: 402. 1951. TYPE: Trinidad. Long Stretch, 15 Jan. 1949, *Simmonds 14256* (holotype, TRIN).

Hemiepiphytic; acaulescent or caulescent, stem appressed-climbing or rarely scandent with slender, whip-like branches bearing small leaves, to 1–6 m long, sap orangish to brownish, sticky, spicy-scented; internodes short, 1–4 cm diam., usually thicker than long, dark green, semiglossy, obscured by cataphyll fibers, roots often many per node, drying dark brown, 2–3 mm diam.; cataphylls sharply 2-ribbed or sharply D-shaped, greenish white, sometimes drying reddish brown, persisting as fibers, margins weakly upturned below. LEAVES erect-spreading; **petioles** 22–70 cm long, 4–11 mm diam., ± D-shaped to sharply C-shaped, broadly sulcate adaxially; **blades** ovate to ovate-triangular, subcoriaceous, moderately bicolorous, acuminate at apex (the acumen sometimes inrolled or very short apiculate, 2–5 mm long), cordate at base, 21.6–59 cm long, 17–37.5 cm wide (1.1–1.7 times longer than wide), (0.7–1.3 times longer than petiole), about equal in length to petiole, upper surface semiglossy, lower surface semiglossy; anterior lobe 19.5–49 cm long, 17–39 cm wide, (2.1–3.9 times longer than posterior lobes); posterior lobes 5–16.5 cm long, 10–18.3 cm wide, obtuse to rounded; midrib broadly sunken, paler than surface above, convex, bluntly angular, paler than surface below; basal veins (3)4(5) per side, with (0)1(2) free to base, 1–2 coalesced 1–4 cm; posterior rib not naked or naked 1–4 cm along the sinus; primary lateral veins 3–6 per side, etched-sunken above, convex below; interprimary veins visible and discontinuous above; minor veins visible and darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect to semi-erect, 2 per axil; peduncle 3–13.5(17) cm long, 3–15 mm diam.; **spathe** 8.5–19 cm long, (1.2–3.6 times longer than peduncle); spathe blade white to greenish, rarely reddish outside, white to greenish inside; spathe tube reddish to dark maroon outside, red to maroon inside; **spadix** stipitate 3–4 mm long; cylindrical, 9–16 cm long, ± uniform throughout; pistillate portion cylindrical, 2.5–5 cm long, 1.4 cm diam. throughout, 1.6 diam. at apex, 1.8 cm diam.

at middle, 1.5 cm wide at base; staminate portion 6.3–7.8 cm long; fertile staminate portion creamy white, cylindrical, to 1.3 cm diam. at base, 1.4 cm diam. at middle, 1 cm diam. ca. 1 cm from apex, broadest in the middle and as broad as the pistillate and sterile portions; sterile staminate portion as broad as or broader than the pistillate portion, 1.2–1.5 cm diam.; pistils 3.2–3.5 mm long, 2.1–2.9 mm diam.; ovary 6–10-locular, with axile placentation; locules 1.6–2.3 mm long; ovules (24)32–36 per locule, 2-seriate, 0.2–0.3 mm long, ± equal in length to funicle; funicle 0.2–0.3 mm long, style similar to style type D; stylar canals emerging into conspicuous depressions; style apex slightly concave to flat; stigma subdiscoid (brush-like), unlobed, 2.1–2.7 mm diam., 0.5–0.7 mm high, covering entire style apex, inserted on entire style apex; the androecium 4–6-sided; thecae slightly obovate, 0.2–0.4 mm wide; sterile staminate flowers ellipsoidal to globose, 2.2–3 mm long. INFRUCTESCENCE with stipe of spadix maroon; berries usually bright red to purple-red, sometimes orange, rarely yellowish white (*McPherson 14496*) to white (*McPherson 11380*).

Flowering in *Philodendron fragrantissimum* in both Panama and Middle America occurs during the rainy season from May to October (except September). Some post-anthesis collections from Middle America are scattered in the dry season as well (January and March). Post-anthesis collections are also principally from May through December (except October) as are immature fruiting collections (July through November). Mature fruits have been collected during May through December (except July and August).

Philodendron fragrantissimum ranges from Belize to Panama along the Caribbean coast and to Pacific Colombia (Chocó), then disjunctly to the Amazon basin, where it ranges from Venezuela to the Guianas, northern Brazil (Roraima and Amazonas), southern Colombia (Meta, Caquetá, Guajira, and Vaupes), and Peru (Amazonas, Loreto, Ucayali, and Madre de Dios). It is also known from Cuba and Trinidad, and it is to be expected in Ecuador and western Brazil. Ranging from near sea level to 1000 m elevation, this species occurs in *Tropical moist forest, Premontane wet forest,* and *Tropical wet forest* life zones.

Philodendron fragrantissimum is a member of *P.* sect. *Philodendron* subsect. *Macrolonchium.* This species is distinguished by its short internodes; a tendency to produce slender, whip-like branches from near the apex; persistent, reddish brown cataphyll fibers; more or less D-shaped petioles with somewhat elevated, lateral margins; ovate to ovate-triangular, cordate blades (about equal to the petioles in length); and colorful inflorescences with the spathes bright red on the tube and white on the blade.

Philodendron fragrantissimum is not easily confused with any other species in Central America, since the combination of D-shaped petioles, persistent cataphylls, and red and white inflorescences is unique, but it has been confused with the Venezuelan *P. chimantae* G. S. Bunting, which differs in having typically more triangular petioles that are actually winged (not merely ribbed) on the lateral adaxial margins, brown cataphylls persisting intact for a time before falling off, and blades with a much narrower sinus.

Philodendron fragrantissimum populations in South America, particularly in the Guiana region (the type locality), have nearly triangular rather than D-shaped petioles typical of those in Central America. In addition, the blade shape is more nearly triangular than ovate as in Central America. I believe, nevertheless, that differences between Central American and South American populations do not warrant taxonomic recognition.

Additional specimens examined. BELIZE. **Cayo**: along Hummingbird Highway at Mile 28, *Dwyer 11411* (MO); Mile 34, *Gentle 9180* (LL). **Stann Creek**: Middlesex, *Gentle 2951* (CM, MICH, RSA). **Toledo**: Punta Gorda–San Antonio, 1 mi. E of junction with road, 100 ft., *Croat 24510* (MO). COSTA RICA. **Alajuela**: Cañas–Upala, near Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, *Croat 36361* (MO). **Cartago**: Tucurrique, Las Vueltas, 635–700 m, *Tonduz 13313* (G, US). **Heredia**: Zona Protectora, N slopes of Volcán Barba, along Quebrada Cantarana, 300–400 m, *Grayum & Schatz 3179* (DUKE); La Selva, 100 m, *Grayum 2436* (CR, MO); Río Sarapiquí, S base of Cerros Sardinal, Chilamate de Sarapiquí, 80–110 m, 10°27′30″N, 84°04′W, *Grayum & Hammel 5541* (MO). **Limón**: Cantón de Talamanca, Amubri, 100 m, 9°31′N, 82°58′W, *Hammel et al. 17512* (CR, MO); Barra del Colorado, 0–2 m, 10°47′N, 83°55′W, *Stevens 24119* (CR, MO); Río Colorado, 1–5 m, 10°47′40″N, 8°35′30″W, *Davidse & Herrera 30922* (CR, MO); Manzanillo de Talamanca, ca. 5 m, 9°38′N, 82°39′W, *Grayum & Burton 4327* (MO); Fila Dimat–Río Uren, Finca de Hermógenes Pereira, *Gómez et al. 23760* (MO, PMA); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8872* (RSA), *8641* (RSA), *8370* (MO, RSA), *Davidson et al. 6766* (MO, RSA). **Puntarenas**: Piedras Blancas–Rincón, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67652* (MO); 10 km W of highway, 200 m, *79169* (INB). GUATEMALA. **Izabal**: ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41810* (GUAT, MO). HONDURAS. **Atlántida**: Parque Nacional Pico Bonito, ca. 10 km SW of La Ceiba, 220 m, 15°42′N, 86°50′W, *Evans 1647* (MO); 80–180 m, 15°42′N, 86°51′W, *Liesner 26183* (MO). **Yoro**: Cordillera Nombre de Dios, S of San José de Texíguat, 250–350 m, 15°30′N, 87°26′W, *Davidse et al. 34398* (MO). NICARAGUA. **Jinotega**: Río Bocay, Caño Litutus,

175 m, 13°58′N, 85°21′W, *Stevens 16680* (MO). **Zelaya**: Comarca del Cabo, Miguel Bikou, *Robbins 5874* (F, GH, MO, NY); Bluefields, *Neill 2587* (MO); Monkey Point, Caño El Pato, 10 m, 11°35′N, 83°42′W, *Moreno 12464* (MO); ca. 13 km above Kururia, 200 m, *Pipoly 3833* (MO); ca. 13 km above Kururia (ca. 14°39′N, 84°04′W), on road to San Jerónimo (14°42′N, 84°11′W), 200 m, *Pipoly 3835* (MO); *3838* (MO); Colonia Kururia, 50 m, 14°41′N, 84°04′W, *Pipoly 3884* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–300 m, 13°40′N, 84°30′W, *Pipoly 4967* (MO); near Tala Has and Puente Mango (over Río Kisalya), 40–60 m, 14°41′N, 84°03′W, *Stevens 7627* (MO); Rosita–Puerto Cabezas, ca. 15.7 km SW of Río Kukalaya, 100 m, 13°58′N, 84°12′W, *Stevens 8526* (MO); Mina Nueva América Road, ca. Km 10, *Stevens 12663* (MO); El Empalme–Limbaika, vic. of road to Alamikamba, ca. 25 m, 13°32′N, 84°30′W, *Stevens 12738* (MO); ca. 1.5 km SE of Palmera, 60 m, 13°35′N, 84°20′W, *Stevens 12847* (MO); Bahía de Bluefields, Round Cay, 0–15 m, 11°56′N, 83°45′W, *Stevens 20069* (MO); Bluefields, Río Escondido, *Molina 2019* (F); at junction of road to Alamikamba, ca. 25 m, 13°32′N, 84°30′W, *Stevens 21747* (MO); Río Troncera, Waspam–Puerto Cabezas, 200 m, 14°43′N, 84°06′W, *Pipoly 4056* (MO); Comarca El Cabo, Pine Savannas, *Molina 15043* (F). PANAMA. **Bocas del Toro**: Chiriquí Grande, near Rambala, 250 m, 8°45′N, 82°15′W, *McPherson 11148* (M, MISSA, MO); Chiriquí Lagoon, *von Wedel 1148* (GH, MO). **Canal Area**: Pipeline Road, Km 5.6, *Witherspoon 8606* (MO, SEL); 150 m, *Nee 6589* (MO, RSA, US); *6591* (MO); Summit Gardens, *Croat 10891* (F, MO, NY, SCZ); Frijoles, *Standley 27477* (US); Ft. Randolph, *Standley 28728* (US); Cerro Pelado, 1 km N of Gamboa, 200–220 m, *Nee 7769* (MO, US); Cerro Viejo vicinity, on K16C, *Blum 1273* (FSU, MO, PMA); Camp Piña, Ft. Sherman, *Duke 4427* (MO); Barro Colorado Island, *Kenoyer 184* (MO); *185* (US); *Fairchild 3080* (US); *Croat 6769* (MO); *4529* (MO); *11857* (MO); *11007* (MO); *10911* (MO, SCZ); *9042* (MO); *9410* (MO); *Netting 44* (MO); ca. 400 m, *Wetmore & Abbe 110A* (MO); *Shattuck 33* (F); *Croat 9003* (MO); *6658* (MO, PMA, SCZ). **Coclé**: Llano Grande–Coclesito Road, Mile 12, 200 m, 8°47′N, 80°28′W, *Churchill et al. 3995* (MO); Penonomé–Coclecito, above Río Cascajál, 5.7 mi. N of Llano Grande, 210 m, 8°40′N, 80°26′W, *Croat 67542* (MO); El Valle region, La Mesa, 880 m, *Croat 37574* (MO); 850 m, *Wilbur et al. 15669* (MO). **Colón**: Miguel de la Borda, *Croat 10014* (MO); Nuevo Tonosí–Río Indio, on road from Portobelo and Nombre de Dios, ca. 0 m, *Croat 33539* (MO); Río Indio–Miguel de la Borda, *Croat 36922* (MO); *Tyson et al. 4546* (MO, SCZ); Santa Rita Ridge Road, Km 21–16, 500–550 m, 9°25′N, 79°37′W, *Knapp 5851* (B, MO); Km 21, 400–500 m, 9°26′N, 79°38′W, *Knapp & Schmalzel 1797* (MO); Km 18–20, 1000–1200 ft., 9°24′N, 79°39′W, *Sytsma 2035* (MO, PMA); Km 16–18 km from highway, 300–400 m, 9°26′N, 79°37′W, *Knapp 1773* (CM, K, MO). **Darién**: Puerto St. Dorotea, *Duyer 2256* (MO); Alturas de Nique Region, S of El Real, near Cana Mine, 550 m, 7°45′N, 77°40′W, *McPherson 11496* (CAS, MO, PMA, RSA); trail NW of Cana, 600 m, *Sullivan 669* (MO); Cerro Pirre region, along trail from base camp to Rancho Frío on slope of Cerro Pirre, 200–450 m, 7°58′N, 77°43′W, *Croat & Zhu 77120* (MEXU, MO, PMA). **Panamá**: Cerro Jefe region, 5 mi. above Inter-American Highway on road to Cerro Azul, *Croat 11526* (F, MO, NY, SCZ, UC); 3.5 mi. W of Lago Cerro Azul, *Croat 11566* (MO); 5.8 mi. above Lago Cerro Azul, 840 m, 9°13′N, 79°22′W, *J. Miller & L. Miller 888* (MO, NY); Cerro Jefe region, 10 mi. from Tocumen Circle, 800–1000 m, *Gentry 2894* (F, MO); 10 mi. from highway, *Croat 15188* (MO); Km 10.1, 300 m, 9°20′N, 79°W, *Croat & Zhu 76548* (MO); near summit, 750–800 m, 9°14′N, 79°22′W, *Croat 67095* (MO); *Witherspoon & Witherspoon 8551* (MO); 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76613* (MO, PMA, US); El Llano–Cartí Road, Km 5–6, 350–375 m, *Croat 34800A* (MO); 7 mi. from highway, 460 m, 9°19′N, 79°59′W, *Croat 75107* (MO, PMA); ca. 8 km N of turnoff, 300 m, 9°16′N, 78°57′W, *Churchill 3810* (MO, RSA); 5 km N of highway, 300 m, *Nee 7915* (GH, MO); along trail to Cerro Brewster from Río Pacora Valley, 670 m, 9°20′N, 79°15′W, *McPherson 7503* (MO). **San Blas**: El Llano–Cartí Road, 34–38 km from Pan-American Highway, 100–200 m, 9°25′N, 79°W, *Knapp & Schmalzel 5467* (MO); km 26.5, 200 m, 9°19′N, 78°55′W, *de Nevers et al. 7839* (GH, MO, US); NW of Nusagandi on Sendero Wedar, 150–200 m, 9°15′N, 79°W, *McPherson 11049* (MO). **Veraguas**: Boca de Concepción, in Golfo de los Mosquitos, 10 m, 8°50′N, 81°W, *McPherson 11380* (CM, M, MBM, MO).

Philodendron gigas Croat, sp. nov. TYPE: Panama. San Blas: El Llano–Cartí road, 10.1 mi. N of Inter-American Highway, then 1.9 mi. N of Nusagandi, 310 m, 9°20′N, 79°W, 20 July 1994, *Croat & Zhu 76988* (holotype, MO–4619563–69; isotypes, B, CAS, CM, COL, CR, F, K, MEXU, NY, PMA, QCNE, VEN, SCZ, US). Figures 192–196, 205.

Planta hemiepiphytica; internodia 1–2 cm longa, (3)6–10 cm diam.; cataphylla acute D-formata, 30–50 cm longa, in sicco rubribrunnea persistentia ut grasso reticulo fibrarum et frustris epidermidis; petiolus semiteres, (59)98–137 cm longus; lamina ovata vel late ovata, cordata vel sagittata basi, (44)81–125 cm longa, (30)37–90 cm lata, in superficie superiore velutina; inflorescentia usque 7; pedunculus 13–16.5 cm longus; spatha 13–16.5 cm longa; lamina spatha alba extus, suffusa rubella atrirubriviolacea; tubo spathae extus purpurascentiviolaceo, intus atripurpascentiviolaceo; pistilla 4–5-locularia; loculi 20-ovulati; baccae viridalbae aut alba.

Hemiepiphytic, growing to 15–20 m; stem appressed-climbing (or scandent when pre-adult), sap reddish, viscous, leaf scars conspicuous, to 4 cm wide; internodes short, 1–2 cm long, (pre-adult length to 15 cm long), (3)6–10 cm diam., glaucous, olive-green to dark green, coarsely white striate near apex, the epidermis with reddish brown patches and reddish brown raised ridges, becoming brown and scurfy, ridged; roots scurfy, short and blunt, dark reddish brown, 5–11 mm diam., feeder root to 3 cm diam., grayish, sparsely and conspicuously warty; cataphylls 30–50 cm long, to 25–30 cm broad at base (when flattened out), ± D-shaped, unribbed to sharply 2-ribbed (ribs low), greenish white to reddish, thick, juicy, drying reddish brown, persisting semi-intact, eventually as a reticulum of fibers and patches of epidermis; **petioles** (59)98–137 cm long, (1.5)2–3 cm diam., subterete, medium

to dark green, semiglossy, weakly and obtusely flattened adaxially, especially near apex, surface densely and finely short-lineate to faintly striate; **blades** ovate to narrowly ovate, moderately coriaceous, bicolorous, acuminate at apex (the acumen weakly inrolled), cordate to sagittate at base, (44)81–125 cm long, (30)37–90 cm wide (1.4–1.7 times longer than wide), (0.9–1.2 times longer than petiole), subcoriaceous, margins hyaline, upper surface dark green, velvety, matte, lower surface slightly paler, semiglossy to matte, sometimes tinged pale reddish between veins; anterior lobe 33–102 cm long (3.5–6.1 times longer than posterior lobes); posterior lobes 13–26 cm long, 13–24 cm wide, incurved and overlapping with sinus closed on adult plants, obtuse; midrib flat to weakly convex, silvery-white to yellowish green, paler than surface above, narrowly rounded and slightly paler than surface below; basal veins (3)9–12 per side, first and second free to base, most of remainder coalesced to 4 cm, 2 coalesced to 14 cm; posterior rib naked 1.5–4 cm; primary lateral veins (4)7–10 per side, departing midrib at a 40–60° angle, arcuate to the margins, narrowly weakly sunken and slightly paler than surface and marginally discolored above, prominently round-raised, paler than surface below; minor veins weakly visible but not distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES (postanthesis) to 7 per axil; peduncle 13–16.5 cm long, green, white-striate, especially at apex; prophylls to 22 cm long; **spathe** 13–16.5 cm long, 5 cm diam., moderately constricted above the tube, weakly glossy; spathe blade 5.8 cm long, white, tinged reddish outside, dark red-violet inside; spathe tube oblong-ellipsoid, 7.5 cm long, purplish violet, short white lineate outside, dark violet-purple, short white lineate inside; **spadix** sessile; to 12.5 cm long, ca. 1.5 cm diam., constricted above sterile portion; pistillate portion pale green, ± ovoid, 4.2 cm long in front, 3.4 cm long in back, 2.2 cm diam.; staminate portion 11 cm long; fertile staminate portion to 2.5 cm diam. midway; sterile staminate portion 2.4 cm diam., slightly broader than pistillate portion; pistils 4–6 mm long, 1.4 mm diam.; ovary 4–5-locular, with ± axile placentation; locules 2.8–5.2 mm long; ovules ca. 20 per locule, 0.1–0.25 mm long, funicle shorter than to equal in length to ovules, style similar to style type B; style crown domed, irregularly lobed; stigma hemispheroid, 1–1.2 mm diam., 0.4–0.7 mm high. INFRUCTESCENCE with berries greenish white; seeds 3–4 per locule, 1.6 mm long.

Flowering in *Philodendron gigas* occurs during the rainy season beginning in about July and probably lasting for more than one month, perhaps as much as two months. Immature fruits have been collected in March.

Philodendron gigas is endemic to the Canal Area, where it is known only along the El Llano–Cartí road in both Panamá Province and in the Comarca de San Blas at 300 to 375 m in *Premontane wet forest* and *Tropical wet forest.*

Philodendron gigas is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Velutina.* This species is distinguished by its appressed-climbing habit; short, thick internodes (6–10 cm diam.); sharply D-shaped, semi-persistent cataphylls; subterete petioles; thick, scaly roots; and especially by its huge, ovate, velvety, dark green leaf blades. It is found growing high on trees, to about 20 m.

Philodendron gigas is apparently most closely related to *P. andreanum* Devansaye from Colombia. That species shares with *P. gigas* dark green, velvety leaf blades, but differs in having more elongate ovate-triangular blades with the lobes much longer than broad (vs. rounded and about as long as broad on *P. gigas*). *Philodendron gigas* has blades about 1.6–2.5 times longer than broad, vs. 2.6–3 times for *P. andreanum.* In addition, *P. andreanum* is described as having the spathe tube green outside and becoming whitish within. In contrast, *P. gigas* has the post-anthesis spathe tube purplish both inside and outside.

Philodendron gigas is not easily confused with any of the other velvety-bladed species of *Philodendron* from Central America. *Philodendron verrucosum* L. Mathieu ex Schott and *P. squamipetiolatum* Croat have velvety blades, but both have scaly petioles. In South America, two other species with velvety, ovate leaf blades, *P. gloriosum* André and *P. mamei* André, differ in being terrestrial with repent stems. Both are probably restricted to the eastern slopes of the Andes.

Additional specimens examined. PANAMA. **Panamá**: El Llano–Cartí Road, Mile 8.2, 300–350 m, *Croat 33680* (B, F, L, MEXU, MO, PMA, QCA, US); Mile 5–6, 350–375 m, *Croat 34778* (F, MO); Mile 10, *Croat 33714* (F, MO). **San Blas**: El Llano-Cartí road, Mile 14, 300 m, 9°15′N, 79°W, *Croat 69242* (CM, MO).

Philodendron glanduliferum Matuda, Bol. Soc. Bot. México 27: 47. 1962. TYPE: Mexico. Oaxaca: Sierra de Juárez, along Hwy. 175, 1900 m, 15 Sep. 1961, *Matuda 37247* (holotype, MEXU). Figures 180, 200–202.

Terrestrial; stem to 1 m long; internodes short, to 8 cm long, to 2 cm diam., about as long as broad

or sometimes broader than long, dense; roots drying 2–3 mm diam., dark reddish brown, folded into irregular longitudinal ribs; cataphylls fleshy, sharply 2-ribbed, reddish, drying pale yellowish brown to brown, persisting semi-intact as a reticulum of fibers which are persistent; **petioles** 44–51 cm long, 3–6 mm diam., subterete, obtusely flattened near base adaxially, often purple at apex, surface inconspicuously short-lineate to striate, prominently so toward apex, with moderately dense, hair-like scales, at least near apex, scales many times longer than wide; geniculum darker than petiole; **blades** ovate-cordate, subcoriaceous, bicolorous, abruptly acuminate at apex (the acumen sometimes apiculate, 2–4 mm long), cordate at base, 34–47 cm long, 1.2–1.4 cm wide (1.2–1.4 times longer than wide), (0.6–0.8 times the petiole length), upper surface semiglossy, lower surface glossy, paler; anterior lobe 24–36 cm long, 11–28(38) cm wide (0.9–1 times longer than wide), (1.9–2.7 times longer than posterior lobes); posterior lobes 11–14.5 cm long, broadly rounded to obtuse; sinus spathulate or V-shaped; midrib flat to convex, paler than surface above; basal veins 5–7 per side, with 1–2 free to base, 2–3 coalesced (0.7)1–2.2 cm; posterior rib not naked, to 1.5 cm; primary lateral veins 2–4 per side, departing midrib at a 50–65° angle, sunken, raised below; minor veins arising from both the midrib and primary lateral veins; tertiary veins moderately distinct, darker than surface below. INFLORESCENCES 1–2 per axil; peduncle 9 cm long, 6 mm diam.; **spathe** smooth, 12–13 cm long (1.5–2.6 times longer than peduncle); spathe blade pinkish white outside; spathe tube magenta outside; **spadix** to 12 cm long, remaining in the spathe at anthesis; pistillate portion to 2 cm long, 10 mm diam.; staminate portion to 10 cm long; fertile staminate portion gradually tapered to apex, 10 mm diam. at constriction, scarcely constricted above the sterile staminate portion, narrowly rounded at apex, 11 mm diam. near the middle, 10 mm diam. at constriction; pistils 2 mm long, 1.9 mm diam.; ovary (5)6(7)-locular, locules 1.3 mm long, 0.6 mm diam., with axile placentation; ovules ca. 10 per locule, 2-seriate, 0.5 mm long, longer than funicle; funicle 0.3 mm long, adnate to lower part of partition; style similar to style type D; style apex somewhat rounded to flat; the androecium truncate, margins irregularly 4–5-sided, ca. 0.9 mm long. JUVENILE plants with lower blade surface purplish.

Flowering in *Philodendron glanduliferum* occurs during the rainy season, in June and September (*Moore & Bunting 8889*). Fruiting collections have not been seen.

Philodendron glanduliferum occurs in Mexico, Guatemala, and Venezuela, with *P. glanduliferum* subsp. *glanduliferum* endemic to Mexico and Guatemala. In Mexico, it is known only from the Sierra de Juárez, at 580 to 1900 m elevation in "Bosque mesófilo." It has been collected recently in Guatemala in the Sierra de las Minas in the province of Zacapa. *Philodendron glanduliferum* subsp. *camiloanum* Croat is endemic to Venezuela, where it is known only from the states of Táchira and Apure at 250 to 1200 m elevation in *Tropical wet forest* and *Premontane wet forest* life zones.

Philodendron glanduliferum is a member of *P.* sect. *Philodendron* subsect. *Achyropodium*. This species is characterized by its terrestrial habit; short internodes; sharply two-ribbed cataphylls persisting semi-intact as a reticulum of pale yellowish brown fibers; subterete petioles with an area of moderately dense hair-like glands at least near the apex; and ovate-cordate blades (about three-fourths as long as petioles) with a spathulate or V-shaped sinus (often overlapping in *P. glanduliferum* subsp. *camiloanum*).

Philodendron glanduliferum subsp. *glanduliferum* is not easily confused with any other species in Central America. *Philodendron glanduliferum* subsp. *camiloanum*, endemic to Venezuela, is distinguished from the typical subspecies by having sharply 2-ribbed cataphylls; petioles glandular more or less throughout; and blades with the sinus closed or nearly so with the margins of the lobes overlapping (at least slightly). In contrast, *P. glanduliferum* subsp. *glanduliferum* has unribbed or only weakly 2-ribbed cataphylls, petioles glandular only near the apex, and blades with the sinus V-shaped and the lobes not at all overlapping.

Philodendron glanduliferum may be confused with *P. ornatum* Schott where they occur together in Venezuela. The latter species is distinguished by its appressed-climbing epiphytic habit and typically larger leaves with the petioles merely warty-verrucose (never glandular) near the apex.

Additional specimens examined. GUATEMALA. **Izabal**: Sierra de las Minas, 700 m, *Forther s.n.* (M). MEXICO. **Oaxaca**: Ixtlán, S side of Río Soyolapan, 1230–1260 m, 17°34′40″N, 96°20′W, *Boyle et al. 2583* (CM, MO); Comaltepec, Highway 185, trail from Puerto Antonio to Cuaje, 1280–1725 m, 17°39′50″N, 96°18′05″W, *Boyle & Acosta 3980* (MO); Valle Nacional–Oaxaca, 660 m, *Croat 78709* (CHIP, MO); 13.9 mi. above bridge at Valle Nacional, 2.6 mi. S of Metates, 1165 m, *Croat 47936* (F, MO); 660 m, *39753* (MO); 1220 m, *43909* (F, MO); *39780* (MO); 4.3–6 mi. above bridge, 705 m, 17°44′N, 96°19′W, *Croat & Hannon 65544* (B, MEXU, MO, US); 6–14 mi. from bridge, 580 m, *Moore & Bunting 8889* (BH, MO); Coatlan–Mazatlan, Cerro Carnero, *MacDougall 335* (MEXU); *409* (MEXU); Tuxtepec–Oaxaca, 55 km S of Tux-

tepec, 630 m, 17°37′N, 96°20′W, *Hammel & Merello 15481* (MO); Tuxtepec, Tuxtepec–Oaxaca, 4 km SE of Metates, *Torres et al. 7811* (MO).

Philodendron grandipes K. Krause, in Engl. & K. Krause, Das Pflanzenr. IV. 23Db (Heft 60): 48. 1913. TYPE: Panama. Colón: Río Fató (Pató) at Dos Bocas (E of Nombre de Dios), 40–80 m, ca. 9°35′N, 79°28′W, *Pittier 4228* (holotype, US). Figures 203, 204, 206, 216.

Philodendron pleistoneurum Standl. & L. O. Williams, Ceiba 3. 109. 1952. TYPE: Costa Rica. Puntarenas: Esquinas Forest, 60 m, 27 Mar. 1951, *Allen 6036* (holotype, EAP; isotypes, GH, US).

Terrestrial; stem creeping over soil, 20–100 cm long, leaf scars obscured by cataphylls; internodes short, 1–4 cm long, 2.8 cm diam., usually broader than long, medium green, semiglossy, coarsely white-streaked at apex; roots ± smooth, slender, elongate, 2–4 mm diam., few per node, descending; cataphylls moderately coriaceous, 16–22 cm long, sharply 2-ribbed, green to pale green or reddish or pinkish, drying brown to tan, persisting semi-intact or as fibers at lower nodes, acuminate at apex. LEAVES arching to pendent; **petioles** 25.5–73 cm long, 10–12 mm diam., D-shaped, spreading, pale to medium green to reddish at base, with a medial rib adaxially, rounded abaxially, with adaxial margins erect, surface finely and weakly striate; sheathing 3.5–5.5 cm long; geniculum slightly thicker than petiole when apparent, 1.4–1.7 cm long, paler than petiole; **blades** broadly ovate-cordate, subcoriaceous, moderately bicolorous, acute to abruptly acuminate at apex (the acumen apiculate and downturned), cordate at base, 20–50 cm long, 15.5–36 cm wide (0.9–1.7 times longer than wide), (0.5–0.9 times the petiole length), broadest at or near the middle, margins broadly undulate, upper surface dark green, semiglossy to glossy, sometimes matte or subvelvety, drying brown to greenish brown, lower surface semiglossy, moderately paler, drying brown to greenish brown; anterior lobe 16–37 cm long, 15–38 cm wide (1.8–3.7 times longer than posterior lobes), broadest slightly above or at point of petiole attachment; posterior lobes 5.5–15.5 cm long, 7.4–18.6 cm wide, directed downward, usually held up somewhat at an angle from the midrib, rounded to obtuse; sinus parabolic to hippocrepiform, sometimes closed with lobes overlapping before being pressed; midrib concolorous, flat at base, becoming weakly sunken toward apex above, thicker than broad at base, becoming convexly raised, concolorous below; basal veins 8–10 per side, 1(2) free to base, several remaining coalesced 0.5–2(4) cm, prominently sunken above, convexly raised below; posterior rib usually not naked, sometimes briefly so at base; primary lateral veins (8–10)11–17 per side, departing midrib at a 20–30° angle, spreading to 50–70° angle, ± straight to the margins, quilted-sunken and concolorous above, prominently convex, matte, and darker than surface below; interprimary veins about as conspicuous as primary lateral veins above, flat and darker than surface below; minor veins arising from both the midrib and primary lateral veins; tertiary veins distinct, weakly raised above, darker than surface below. INFLORESCENCES erect, 2–4 per axil; peduncle 2.5–14 cm long, 5–8 mm diam., terete, green to reddish, white-lineate; **spathe** 6.6–11.8 cm long (0.6–2.5 times longer than peduncle), constricted ± midway; spathe blade lanceolate, pinkish red, tinged green, pale green to white or green, short white lineate outside, 4–6 cm long (opening broadly elliptic in face view), pinkish red to white, pale greenish white or pale green inside; spathe tube oblong-ellipsoid, dark reddish maroon to reddish purple to green, weakly short dark lineate outside, 2.5–4 cm long, 1.4–3.8 cm diam., pale green to greenish white to pinkish red inside; **spadix** sessile or very short stipitate; tapered, 6.6–11.8 cm long, broadest near the base; pistillate portion white, yellowish white (post-anthesis), slightly tapered toward the apex and base, (1.6)2–2.7 mm long, 9–11 mm diam. at apex, 1–1.5 cm diam. at middle, (6)10–11 mm wide at base; staminate portion 3.5–7.1 cm long; fertile staminate portion white, cylindrical to tapered, 7–10 mm diam. throughout, 1–1.5 cm diam. at base, 7–10 mm diam. at middle, 4–6 mm diam. ca. 1 cm from apex, narrower than the pistillate portion, as broad as the sterile portion; sterile staminate portion about as the pistillate portion, white, 1–1.5 cm diam.; pistils 1.8–2.3 mm long, 1.1–1.5 mm diam.; ovary (4)5–6-locular, 1.3–1.5 mm diam., locules 1–1.5 mm long, 0.4–0.6 mm diam., with axile placentation; ovules (7–10)16–22 per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle, style similar to style type B; style apex ± concave, sometimes weakly lobed; stigma subdiscoid, brushlike, lobed or unlobed, 0.9–1.4 mm diam., 0.2–0.5 mm high, covering center of style apex, depressed medially; the androecium truncate, margins irregularly 3–6-sided; thecae oblong, 0.2–0.3 mm wide; sterile staminate flowers blunt, margins irregularly elongate, 13–18 mm long, 9–13 mm wide. Berries creamy white, obovoid, apex truncate; seeds 20 per locule, 1.9 mm long, 0.2 mm diam., with prominent striations running from funicle to apex and slightly spiraling, perpendicular to larger veins. JUVENILE

blades narrowly elliptic to ovate, acute to weakly cordate at base.

Flowering in *Philodendron grandipes* probably occurs throughout most of the year (February through November, except October) but primarily in July and August. Post-anthesis collections have also been made throughout the year, and immature fruiting collections are known from throughout the year (except February, March, and June).

Philodendron grandipes ranges from Nicaragua (Zelaya) to Panama, Colombia, and Ecuador (Esmeraldas), from near sea level to mostly less than 750 m (sometimes to 1200 m) elevation in *Tropical moist forest, Premontane wet forest,* and *Tropical wet forest* life zones.

Philodendron grandipes is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is characterized by its terrestrial habit, short internodes, persistent cataphyll fibers, broadly ovate-cordate leaf blades, usually green spathes, and, especially, by its D-shaped petioles with erect margins and a medial adaxial rib.

Philodendron grandipes is closest to *P. jodavisianum,* which has a similarly shaped petiole and other general features in common. The latter species differs in being an appressed-climbing hemiepiphyte with ovate-triangular (rather than broadly ovate) blades.

This species frequents stream banks in central Panama and is one of the few consistently terrestrial *Philodendron* species in Central America. Habitat in Costa Rica, however, is variable. *Philodendron grandipes* occurs along stream banks on the Osa Peninsula, but at La Selva (Heredia) this species is widely scattered in the forest understory (M. Grayum, pers. comm.).

Spathe tube color in this species is variable to some extent geographically. For example, on the Atlantic slope of Costa Rica the spathe tube is usually greenish, whereas on the Pacific slope it is generally reddish on both surfaces.

Additional specimens examined. COSTA RICA. **Alajuela**: 36–37 km NW of San Ramón, 500–515 m, 10°15′N, 84°34′W, *Croat 68198* (MO); Río Chiquito, Upala, 800 m, *Gómez 18639* (MO, PMA). **Heredia**: Tirimbina, 230 m, *Proctor 32347* (LL); 1 km SE of Tirimbina, 220 m, *Lent 2136* (CR, F, MEXU, MO); near Río Bijagual, 2 km E of Tirimbina, 150 m, *Maas 1329* (U); Porto Viejo–Río Sucio, 20 m, *Croat 35676* (CR, MO); La Selva Field Station, 100 m, *Grayum 3028* (DUKE), *Folsom et al. 8806* (DUKE), *Hammel 9126* (DUKE), *Sperry 855* (DUKE), *Croat 44254A* (MO), *44224* (MO), *Cannarella 8806* (DUKE), *McDowell 687* (MO), *Grayum et al. 1758* (F, MO), *Jimenez IV* (MO), *VII* (MO). **Limón**: Braulio Carrillo–Guápiles, 250–270 m, *Croat 78745* (CR, INB); Toro Amarillo, 10 km W of Guápiles, 300 m, *Lent 73* (F); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8741* (MO, RSA); Turrialba–Limón, along Hwy. 32, ca. 11 mi. S of Siquirres, 650 m, *Croat 43330* (MO); Río Chirripó–Río Corinto, N of Quebrada El Molinete, 400 m, 10°12′N, 83°54′W, *Grayum & Jacobs 3525* (MO); Quebrada Cañabral–Río Barbilla, 200–400 m, 10°02′N, 83°26′W, *Grayum et al. 8739* (CR, MBM, MO); Hitoy Cerere Reserve, 140 m, 9°42′N, 83°02′W, *Hammel & Grayum 14349* (MO); Parque Nacional Tortuguero Lomas de Sierpe, near Río Sierpe, 100 m, 10°24′N, 83°33′W, *Robles et al. 2006* (CR, G, MO); Río Blanco, Río Frío–Limón, W of Guápiles, Quebrada Danta, 360 m, 10°12′N, 83°49′W, *Croat 68419* (MO); Río Catarata, 50–100 m, 9°37′N, 82°49′W, *Burger & Antonio 10888* (CR, F, MO, PMA, U); Río Colorado, 16 airline km SW of Barra del Colorado, 10–120 m, 10°39′N, 83°40′40″W, *Davidse & Herrera 31214* (CR, K, MO); Río Sixaola, ca. 3 mi. NE of Bratsi, 15 m, *Croat 43253* (CR, MO); 0.3 mi. E of Bratsi, ca. 35 mi. SE of Limón, 30 m, *Croat 43289* (MO); Limón–Shiroles, 6.5 mi. SW of Bribrí, 50 m, *Croat 43299* (CR, MO); Pococí, Barra del Colorado, Llanura de Tortuguero Sardinas, 15–20 m, 10°38′38″N, 83°44′10″W, *Araya 596* (INB). **Puntarenas**: Osa Península, Piedras Blancas–Rincón, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67651* (K, MO); 2.5 mi. SW of Rincón, 8°42′N, 83°29′W, *Kennedy 1622* (MO); *Croat 76751* (MO); Rincón de Osa, 250–540 m, 8°42′N, 83°31′W, *Croat & Grayum 59838* (MO); SW of Rincón de Osa, 40–200 m, 8°42′N, 83°30′W, *Grayum et al. 7555* (CR, M, MO); Fila Costeña, 950–1150 m, *Grayum 10651* (CR, INB); Cortu–La Unión, near San Miguel, *Croat 26519* (MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1150 m, *Croat 22262* (MO); *Allen 6036* (F, GH); Finca El Edén, km 183, ca. 400 m from Santa Marta, *Gómez 22954* (MO); Corcovado National Park, Sirena, 0–200 m, 8°29′N, 83°36′W, *Liesner 2903* (MO); 5–25 m, 8°29′N, 83°34′W, *Hammel & Kernan 16662* (CR, MO); 150 m, *Kernan & Phillips 512* (CR, MO); Rancho Quemado, 250–350 m, *Marín 39* (CR, INB, MO); vic. Boscosa, 50 m, *Croat & Hannon 79244* (MO); Las Cruces Tropical Botanical Garden, 1200 m, 8°49′N, 82°58′W, *Croat 57234* (CR, MO); Río Jaba, Las Cruces, 1200 m, *Meerow et al. 2017* (SEL). **San José**: San Isidro del General–Dominical, SW of San Isidro, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35215* (MO); 9 mi. SW of Río Pacuare, 680 m, *Croat 35346* (MO); 12 km SW of San Isidro de El General, along CR-223, 900–1000 m, *Utley & Utley 4925* (MO); 14.5 km S of San Isidro del General, 500 m, *Kress & Gómez 88-2467* (SEL); Zona Protectora La Cangreja, ca. 2 km NNE of Mastatal de Puriscal, 400–540 m, 9°42′N, 84°22′W, *Grayum 8644* (MO); Parque Nacional Braulio Carillo, above Río Sucio, 5–600 m, *Pennington 11533* (K); 1100 m, 10°24′04″N, 85°03′03″W, *Carballo 87* (CR, MO). NICARAGUA. **Zelaya**: 150–180 m, 11°43′N, 84°18′W, *Stevens 4965* (MO); Río Rama, at Salto La Oropendola, 15–25 m, 11°57′N, 84°17′W, *Stevens 8960* (MO). PANAMA. **Bocas del Toro**: Chiriquí Grande–Fortuna, 13.2 mi. W of Chiriquí Grande, 310 m, 8°45′N, 82°10′W, *Croat & Grayum 60141* (MO); ca. 10 km SW of Chiriquí Grande, ca. 300 m, 8°52′N, 82°10′W, *Thompson 4938* (CM, MO); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat 60264* (CM, MO); 450 m, 8°45′N, 82°15′W, *McPherson 7369* (MO); 3 mi. N of Continental Divide, 650 m, 8°47′N, 82°11′W, *Churchill & Churchill 6209* (MO); *6210* (MO); Chiriquí Lagoon, *von Wedel 1049* (F, GH, MO). **Canal Area**: Gamboa, *Standley 28401* (US); Frijoles, *Standley 27471* (US);

Barro Colorado Island, *Standley 31361* (US); *40888* (US); *Croat 16574* (MO); *12300* (MO, SCZ); *11886* (MO); *11194* (MO); *11077* (MO); *9526* (MO); *6512* (MO); *5117* (MO); *Schmalzel 849* (MO); Summit Gardens, *Croat 11491* (MO). **Chiriquí**: Chiriquí Grande–Fortuna, 7.7 mi. W of Chiriquí Grande, 80 m, 8°50′N, 82°10′W, *Croat & Grayum 60114* (MO); Burica Peninsula, San Bartolo Límite, 12 mi. W of Puerto Armuelles, 400–500 m, *Croat 22188* (MO). **Coclé**: La Junta–Limón, 5 hours walk N of Alto Calvario, 800–1000 m, *Folsom 5861* (MO); Coclesito–Llano Grande, 200 m, 8°47′N, 80°28′W, *Churchill et al. 4170* (MO); El Valle region, 800–900 m, 8°36′N, 80°07′W, *Croat & Zhu 76664* (MO, PMA); *67212* (F, MO); 800 m, *25406* (F, MO); ca. 1000 m, *Gentry 5662* (F, MO); *Croat 14391* (MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76710A* (MO); 860–900 m, *Croat 37398* (MO, RSA); Cerro Pilón, *Duke & Dwyer 13977* (MO). **Colón**: Portobelo–Nombre de Dios, 6–8 km from Peluca Hydrographic Station, *Kennedy & Dressler 3331* (US); Portobelo–Río Cascajal, vic. of Nuevo Tonosí, *Croat 33648* (K, MO, US); 6 mi. S of Portobelo, *Croat 11401* (MO); Portobelo–Nombre de Dios, 1.2 mi. beyond junction of road to Isla Grande, 9°40′N, 79°35′W, *Croat 49795* (MO); Altos de Pacora–Cerro Brewster trail, 700 m, 9°18′N, 79°16′W, *de Nevers et al. 6234* (MO); Río Guanche, 0.5–1 km upstream from Puerto Pilón–Portobelo road, 6 km S of Portobelo, 5–30 m, *Nee 7153* (MO, US); ca. 3–5 mi. inland, 10–100 m, *Croat 26205* (MO); 30–100 m, *79345* (PMA, MO); 1.5 mi. upstream, ca. 10 m, *Kennedy & Dressler 1513* (SEL); <100 m, 9°27′N, 79°40′W, *Croat & Zhu 76245* (MO); Río Miguel de la Borda, vic. of Guásimo, *Croat 9940* (MO). **Darién**: Cerro Pirre region, vic. Cana gold mine, 500–600 m, *Croat 37637* (MO); 480 m, *37957* (MO); 17 km N of El Real, trail from base camp along Río Perisenico, 100 m, 8°01′N, 77°44′W, *Croat & Zhu 77177* (MO); Río Cocalito, *Whitefoord & Eddy 132* (BM); Río Tuquesa, ca. 2 km by air from Continental Divide, vic. of Tyler Kittredge gold mine, *Croat 27191* (MO). **Panamá**: El Llano–Cartí Road, 9.6 km from Pan-American Highway, 410 m, *Mori & Kallunki 1835* (MO, PMA); Km 12.4, 300–400 m, *Folsom et al. 6178* (MO, PMA); Km 13.2, 370 m, 9°16′N, 78°57′W, *Hoover 1313* (MO); Mile 5–6, 350–375 m, *Croat 34802* (MO); vic. of Gorgas Lao Mosquito Control Project Site at km 12, *26058* (MO); Serranía de Majé, S of Ipetí, 500–650 m, *Hufi et al. 1692* (MO); Serranía de Cañazas, Rancho Chorro, above Tortí Arriba, 400–700 m, *Folsom 6748* (MO); Cerro Campana, ca. 1 mi. from Inter-American Highway, ca. 150 m, *Croat 35969* (MO, RSA). **San Blas**: El Llano-Cartí Road, trail along Continental Divide, 400 m, 9°20′N, 78°56′W, *McDonagh et al. 323* (BM); SE of Puerto Obaldía, *Croat 16762* (MO); 14 mi. N of Pan-American Highway, 300 m, 9°15′N, 79°W, *Croat 69249* (MO); Miria Ubigandup Island, Digole, 0–20 m, 9°26′N, 78°54′W, *Herrera 292* (MO); Río Playón Chico, vic. NEBA DUMMAT, 100–450 m, 9°14.5′N, 78°15′W, *Herrera et al. 1399* (MO, PMA); 1 mi. S of Nusagandi, Mile 9, 350 m, 9°20′N, 79°W, *Croat & Zhu 76997* (MO, PMA); Nusagandi, 275–300 m, 9°20′N, 79°W, *Croat 76594* (MEXU, MO). **Veraguas**: Santa Fe region, Cerro Tute, 1050–1150 m, *Croat 48907* (MO); Escuela Agrícola Alto Piedra-Calovébora, Río Dos Bocas Valley, N of Santa Fe, 350–400 m, *Croat 27398* (MO); 450 m, *27550* (MO); Escuela Agrícola Alto Piedra–Río Dos Bocas, ca. 10 km from the school, 530–620 m, *Croat 25903* (MO).

Philodendron granulare Croat, sp. nov. TYPE: Panama. Darién: Río Pirre, 14 July 1971, *Croat & Porter 15543* (holotype, MO–2059344; isotype, PMA). Figures 207, 208.

Planta hemiepiphytica; internodia 3.5–4 cm longa, ca. 1 cm diam.; cataphylla acute 2-costata, 15 cm longa, decidua; petiolus 8–9 cm longus, 7–8 mm diam., convexus adaxialiter cum 2 costis marginalibus; lamina oblongo-oblanceolata, debiliter cordata basi, 19–28 cm longa, 4–6 cm lata; nervis primariis lateralibus 5–6 utroque; inflorescentia 1; pedunculus 10.5 cm longus; spatha usque 15.7 cm longa, viridis; lamina spathae intus viridi; tubo spathae extus suffuso rubro, intus rubro; pistilla 3–5-locularia; loculi 1-ovulati.

Hemiepiphytic vine; internodes semiglossy, 3.5–4 cm long, ca. 1 cm diam., longer than broad, drying light brown, epidermis longitudinally deeply ridged, finely striate on magnification and densely granular to almost scabrous (but not harsh to the touch), the vestiture raised to ca. 1.5–2 times longer than wide; roots drying dark brown, <15 cm long, 1 mm diam., few per node; cataphylls 15 cm long, sharply 2-ribbed (ribs low), green, deciduous. LEAVES with **petioles** 8–9 cm long, 7–8 mm diam., convex with acute margins adaxially, drying dark brown and somewhat sulcate adaxially with distinct acute marginal rib; sheath short, inconspicuous, 1–2 cm long, for <0.25 its petiole length; **blades** oblong-oblanceolate, acuminate at apex, weakly cordate at base, 19–28 cm long, 4–6 cm wide (3.8–4.7 times longer than wide), upper surface medium green, weakly glossy, drying dark brown, lower surface slightly paler, drying yellowish brown; midrib flat, concolorous above, convex, slightly paler than surface below; basal veins 1–2 per side, with 1–2 pairs free to base, indistinct; primary lateral veins 5–6 per side, weakly sunken above, convex, slightly paler than surface, drying paler below; minor veins moderately obscure, barely visible on drying, the larger weakly undulate, arising from the midrib only, secretory canals appearing on magnification as short, pale raphide cells along the minor veins. INFLORESCENCES (post-anthesis), 1 per axil; peduncle 10.5 cm long, 1 cm diam.; **spathe** to 15.7 cm long, to 7 cm wide when flat, weakly constricted above the tube, green throughout; spathe blade green inside with prominent striations from lower 1.5 cm to 9 cm up from base; spathe tube tinged red outside, red inside; fertile staminate portion to 5.5 cm long, 9 mm diam.; **spadix** with pistils 1.5–3 cm diam., drying light brown, sparsely granular on the sides; ovary 3–5-locular; ovules with 1 per locule, style similar to style type E; style funnel 0.5–0.7 mm, distinctly raised above the surface. INFRUCTESCENCE 10

cm long, 2.7 cm diam. in lower ⅓, prominently tapered toward apex to 1.3 cm diam. at apex; berries whitish; seeds oblong-elliptic, tan, smooth, 1.3–1.9 mm long.

Flowering in *Philodendron granulare* probably occurs in the early wet season. Fruiting is recorded by a single collection made in July.

Philodendron granulare is known only from the Panamanian type specimen, from Darién Province near El Real along the Río Pirre at less than 75 m elevation in *Premontane wet forest.*

Philodendron granulare is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is distinguished by its scandent habit, more or less oblong, short-petiolate blades with subcordate bases, and especially by its densely granular dried stem (hence the name) and distinct funnel-shaped styles.

Philodendron granulare is most easily confused with *P. bakeri,* which it resembles in a superficial way. The latter species differs in having totally smooth stems, petioles with conspicuous sheaths often extending to the middle or beyond, leaf blades with more conspicuous minor veins, and pistils with a truncate, type B style which lacks a funnel, having instead the stylar canals emerging directly onto the flat truncate apex.

Philodendron grayumii Croat, sp. nov. TYPE: Panama. Bocas del Toro: Fortuna Lake area, Fortuna–Chiriquí Grande, 0.3 km N of Continental Divide, 970 m, 8°43′N, 82°17′W, 27 June 1994, *Croat & Zhu 76524* (holotype, MO–4619417–20; isotypes, AAU, B, CAS, CM, CR, COL, DUKE, F, GH, K, M, MEXU, NY, PMA, S, SCZ, SEL, TEX, US). Figures 209–215.

Planta hemiepiphytica; internodia 1–10 cm longa, (2.5)3.5–7 cm diam.; cataphyllum 11–26 cm longa, incostata vel leniter 1-costatata, demum decidua aut acute complanta vel 2-costata; petiolus 40–97 cm longus, subteres, obtuse planatus prope apicem; lamina ovata vel late ovate, (31)50–73 cm longa, 24–44(58) cm lata; cordata basi; nervis basalibus 4–5(6) utroque; nervis lateralibus I 4–6 utroque; inflorescentia 1–5 per axillam; pedunculus (2)4–6 cm longus; spatha (11)13–16(18) cm longa, extus pallide viridis vel virens, albida vel pallide flava vs. apicem, minimum interdum maculata purpurea-violacea, tubo spathae marronino vel rubro intus; pistilla 7–8-locularia; loculi (2)3–4(5)-ovulati.

Hemiepiphytic, appressed-climbing; internodes semiglossy to matte, 1–10 cm long, (2.5)3.5–7 cm diam., dark green to gray-green or tannish gray, drying brown to yellow-brown or reddish brown, epidermis closely ridged or fissured, sometimes peeling; roots usually 1–2 per node, ca. 3–4 mm diam., drying dark reddish brown; cataphylls thick, somewhat spongy, 11–26 cm long, unribbed to weakly 1-ribbed near apex or sharply flattened to sharply 2-ribbed (ribs close), green, sometimes weakly maroon-spotted, often persisting intact for a short time then deciduous, intact; **petioles** 40–97 cm long, 1–1.5 cm diam., subterete, firm, dark to medium green, obtusely and often weakly flattened near apex, sometimes weakly ribbed near apex adaxially, surface semiglossy, weakly and densely short pale green lineate, drying yellowish brown to dark brown, smooth to finely striate, sheath 6–15 cm long; **blades** ovate to broadly ovate, coriaceous to subcoriaceous, moderately bicolorous, semiglossy, acute to gradually or abruptly acuminate at apex, deeply cordate at base, (31)50–73 cm long, 24–44(58) cm wide ((0.7)1–1.9 times longer than wide), three-fourths as long as to somewhat longer than the petiole, upper surface dark green, drying dark brown to yellow-brown or grayish brown, semiglossy, lower surface conspicuously paler, drying yellow-brown, weakly to semiglossy; anterior lobe (25)31–49(60) cm long, (13)24–32(42) cm wide (2.3–4.6(8) times longer than posterior lobes), margins broadly rounded, sometimes sinuate; posterior lobes rounded to narrowly rounded, sometimes overlapping, (6)9–13(17) cm long, 12–18(22) cm wide; sinus hippocrepiform to oblong spathulate, obovate, or sometimes triangular to parabolic, rounded to narrowly rounded, (8)10.5–13 cm deep; midrib flat to broadly raised above, paler than surface above, convex to obtusely acute and sometimes purplish spotted below; basal veins 4–5(6) per side, with 1–2 free to base, third and higher order veins coalesced 3–6(8) cm long; posterior rib usually not naked, rarely naked for 1.5 cm; primary lateral veins 4–6 per side, departing midrib at a (45)55–70(75°) angle, downturned and splayed out when joining midrib, obtusely to narrowly sunken and paler than surface, sometimes weakly raised, drying weakly ridged near the midrib above, convex and paler than surface, sometimes reddish below; minor veins moderately indistinct, drying weakly prominulous (surface often with minute purplish raised areas seen on high magnification), arising from both the midrib and primary lateral veins, secretory ducts appearing as intermittent lines (less conspicuous on highland forms); INFLORESCENCES 1–5 per axil; peduncle (2)4–6 cm long, 1–1.5 cm diam., pale green, finely short-lineate; **spathe** (11)13–16(18) cm long, 2–3 cm diam. (2.1–2.6(3.5) times longer than peduncle), weakly constricted ± above the middle, pale to medium green, sometimes whitish to pale yellowish toward apex, often tinged or

spotted violet-purple throughout, especially near base, sometimes green dorsally with only the front edges of tube maroon, margins white, outer surface drying reddish brown throughout inside, violet-purple to maroon in lower one-half to two-thirds, especially in lower half; spathe tube 7–8.5 cm long, 2–3.6 cm diam., maroon to red, with pale lineations extending onto blade area inside; **spadix** sessile; cylindrical, 9.5–16 cm long, broadest above the middle or below the middle; pistillate portion pale green, cylindrical to weakly tapered toward the apex, 3.3–3.5 cm long, 4.6 cm long in front, 3.2–3.5 cm long in back, 9–20 mm diam. throughout; staminate portion 6.3–12.5 cm long; fertile staminate portion creamy white, cylindrical, 1–1.4 cm diam. at base, 1–1.4 cm diam. at middle, 8–10 mm diam. ca. 1 cm from apex, broadest at the base or at the base broader than or as broad as the pistillate portion, sterile staminate portion usually not detectable; pistils 1.4–1.9 mm long, 0.8–1.1 mm diam.; ovary 7–8-locular, 1–1.4 mm long, 0.8–1 mm diam., walls thin and membranous, locules 1–1.3 mm long, 0.3–0.4 mm diam., ovule sac sometimes present, to 0.8 mm long, with sub-basal placentation; ovules (2)3–4(5) per locule, 2-seriate, contained within transparent, gelatinous ovule sac, 0.3–0.5 mm long, usually as long as funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.5 mm long, 1.2 mm diam., similar to style type B; style apex sloping; stigma brushlike, sometimes cupullate, subdiscoid, unlobed, sometimes truncate or weakly domed, 0.9–1.3 mm diam., 0.2–0.6 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.9 mm long, 1.1 mm diam. at apex; thecae cylindrical to weakly elliptical, 0.3–0.4 mm wide, ± parallel to one another; sterile staminate flowers trapezoidal to 4–6-sided, 1.1 mm long, 1.3 mm wide. INFRUCTESCENCE with peduncle to 11.5 cm long; spathe to 26 cm long, pistillate spadix to 13.5 cm long, 2.5 cm diam.; staminate spadix to 13.5 cm long; berries pale ochraceous, 3–3.3 mm long; seeds 1.9–2 mm long, 0.7–1 mm diam. PREADULT petioles sheathing throughout; blades oblong, subcordate, 26–31 cm long, 9–13 cm wide.

Flowering in *Philodendron grayumii* apparently occurs primarily in the rainy season (March as well as June and September), but also in the late dry season. Post-anthesis inflorescences have been collected in March and June through August and November. Immature fruits are known from June and November.

Philodendron grayumii ranges from Costa Rica to central Panama from sea level to 1630 m elevation in *Premontane wet forest, Tropical wet forest,* and *Premontane rain forest* life zones, as well as *Premontane wet forest* transition to *Tropical moist forest.*

Philodendron grayumii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* This species is characterized by its yellow-brown-drying stems; cataphylls deciduous intact; more or less ovate blades drying yellow-brown with the basal veins scarcely or not at all united into posterior ribs and rarely naked on the sinus; and primary lateral leaf veins splayed out, somewhat ridged, and downturned near the midrib. The spathe is often tinged reddish to purplish outside and dark red to maroon in the tube within.

This species is polymorphic, especially in the nature of the resin canals in the leaves and the number of inflorescences per axil. Collections from near sea level in Limón Province of Costa Rica (*Grayum 8467, 8469*) are unusual in lacking any clearly visible secretory ducts (normally easily visible at least on the dried lower leaf surfaces).

Philodendron grayumii may be confused with *P. edenudatum,* and the two may prove to be conspecific. *Philodendron edenudatum* differs in having proportionately longer leaf blades (1.8–2.1 times longer than broad) and proportionately shorter petioles (0.77–0.89 times as long as the blades).

Philodendron grayumii may also be confused with *P. ferrugineum.* The latter, occurring principally in the Canal Area, shares with *P. grayumii* brownish-drying blades with the basal veins usually not at all or only weakly naked. *Philodendron ferrugineum* differs in having generally shorter internodes; larger cataphylls (26–48 vs. 11–26 cm long); typically much larger, more coriaceous blades drying reddish brown (rather than yellowish brown); and minor veins usually drying markedly longitudinally raised but interrupted, giving the leaf surface a markedly bumpy, irregular, and uneven appearance.

Also perhaps confused with *P. grayumii* is *P. dodsonii,* which has dried leaf blades of a similar yellowish brown color. The latter species differs in having conspicuously naked posterior ribs, and blades drying matte on the upper surface and lacking any obvious secretory ducts on the lower surface.

Perhaps also confused with *P. grayumii* is *P. aromaticum,* which has similarly cordate blades that may dry a similar color and also has deciduous cataphylls. The latter species is distinguished by being a shorter-stemmed canopy epiphyte, and by having spongy petioles and proportionately more elongated, usually more gray-drying leaf blades

(usually more than 1.7 times longer than wide) with the naked portion of the posterior ribs much longer (usually 2.5–5 cm long).

A noteworthy collection is *Croat 67525*, which is somewhat intermediate between *P. grayumii* and *P. edenudatum*. It has narrowly ovate leaf blades about 1.6 times longer than wide, mottled petioles and lower midribs, and relatively small (possibly immature) inflorescences (to 13 cm long). In these characters, the specimen is closest to *P. edenudatum*, but it has prominent secretory ducts visible on the lower blade surface, and two inflorescences per axil, features not known in *P. edenudatum*. In addition, the blades dry dark brown. In this latter regard, this collection differs from both *P. grayumii* and *P. edenudatum*. It perhaps represents a new species, although it is being included with *P. grayumii* for now.

Another noteworthy collection is *Croat & Zhu 76613*, the only collection from east of the Canal Area. It is unusual in having the cataphylls semipersistent as fibers, rather than deciduous while still intact. This may prove to represent a different taxon.

A sterile collection (*Croat 66712*) is noteworthy in having stems that dry smoother, darker reddish brown, and semiglossy; much glossier petioles than those of *P. grayumii*; and blades that dry more coriaceous, glossier, and with the minor veins prominulous on both surfaces. It might represent another new species, but is tentatively included with this species.

The new species is named in honor of Michael H. Grayum, a colleague and aroid specialist, whose excellent collections of Araceae from Costa Rica and Panama have played an important role in this revision. He has collected the only Costa Rican material of the species.

Additional specimens examined. COSTA RICA. **Limón**: along road between Puerto Viejo de Talamanca and Manzanillo, vic. of Punta Cocles, ca. 5 m, 9°38′N, 82°43′W, 5 m, *Grayum & Sleeper 4302* (CR, MO); 10–20 m, 10°38–39′N, 82°40–44′W, *Grayum 3637* (MO); Piuta, ca. 1.5 km NW of Puerto Limón along highway to Portete, 5 m, 10°01′N, 83°03′W, *Grayum & Hammel 8467* (MO), *8469* (MO). PANAMA. **Bocas del Toro**: Fortuna–Chiriquí Grande, 1.6 mi. N of Continental Divide, 770–790 m, 8°45′N, 82°17′W, *Croat 76456* (AAU, CM, MEXU, MO, NY, OOM); 1.2 mi. N of Divide, 5.3 mi. N of Fortuna Dam, 910 m, 8°44′N, 82°17′W, *Croat 60476* (AAU, CR, MO, PMA), 1170 m, *Croat 66653A* (MO); 5.8 mi. N of Fortuna Lake, 600 m, 8°45′N, 82°18′W, *Croat 66794* (B, CAS, CM, COL, CR, F, K, L, MEXU, MO, NY, PMA, US, WIS); along Continental Divide (4.5 mi. N of middle of bridge over Fortuna Lake), 1170 m, 8°44′N, 81°17′W, *Croat 66712* (MO); Gualaca–Chiriquí Grande, 1.6 mi. N of Continental Divide, 850 m, 8°48′N, 82°13′W, *Croat 74933* (MO); 4.2 mi. E of Chiriquí Grande, ca. 0 m, 8°55′N, 82°09′W, *Croat 66814* (MO, TEX); Station Milla 7.5 on Changuinola–Almirante Railroad, <100 m, *Croat 38105* (B, F, K, MO, NY, PMA, US); Cerro Colorado, 6.5 mi. W of Chame, 1630 m, 8°35′N, 81°50′W, *Croat 69164* (MO); Chiriquí Grande, Palo Seco–El Guayabo, km 112, *Gordon 344* (PMA). **Chiriquí**: Gualaca–Chiriquí Grande, 4 mi. N of bridge over Fortuna Lake, 1200 m, 8°46′N, 82°16′W, *Croat 68026* (CAS, CR, DUKE, F, G, MO, QCA, TEX, W); 1170 m, 8°44′N, 81°17′W, *Croat 66712* (CAS, K, L, MEXU, MO, PMA); Río Hornito, ca. 0.5 km S of Centro de Científicos, 8°45′N, 82°18′W, *Croat 76420* (CM, MO); 8.4 mi. beyond Los Planes de Hornito, 1130 m, 8°44′N, 82°14′35″W, *Croat 67869* (DUKE, MO, NY, PMA). **Coclé**: 4.5 mi. N of El Copé, 580–740 m, *Croat 67525* (C, ENCB, MO, P, VDB); 4.1 mi. N of El Copé, 770–680 m, 8°39′N, 80°36′W, *74840* (CM, CR, MO, PMA, US); 5–6 mi. N of El Copé, 600–800 m, 8°38′N, 80°35′W, *Croat & Zhu 77202* (IBE, M, MO, MY, W); Llano Grande–Coclecito, 4.3 mi. N of stream in Llano Grande, 330 m, *Croat 49235* (CM, MO). **Veraguas**: vic. of Santa Fe, 5 mi. past Escuela Agrícola Alto de Piedra, 670 m, 8°33′N, 81°08′W, *Croat 66922* (BR, COL, M, MO), *66969* (AAU, MO, NY, OOM, PMA).

Philodendron hammelii Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, ca. 6 km N of El Copé, Pacific drainage, on ridge W of sawmill, 850–1100 m, 8°39′N, 80°36′W, *Hammel 3551* (holotype, MO–2658909). Figure 217.

Planta terrestris; internodia 1–1.5 cm longa, 8–12 mm diam.; cataphylla 11.5 cm longa, 1-costata, persistentia ut reticulum tenue fibrarum; petiolus subteres, 31–32 cm longus, 2–3 mm diam., dense obtecta squamis latis, pallidis prope apicem; lamina ovato-cordata, 21–22 cm longa, 13–16 cm lata, in sicco canoviridis supra, flavibrunnea infra; inflorescentia 1; pedunculus 4.5 cm longus, 4 mm diam.; spatha 11 cm longa; pistilla 6-locularia; loculi 14-ovulati.

Terrestrial; internodes 1–1.5 cm long, 8–12 mm diam., drying yellow-brown, semiglossy, conspicuously ridged; roots drying reddish brown to brown, slender, numerous per node; cataphylls to 11.5 cm long, 1-ribbed, drying yellowish brown, thin, smooth (not scaly), persisting as a thin, pale reticulum of branched tan fibers; **petioles** 31–32 cm long, 2–3 mm diam., subterete, drying weakly glossy, smooth or at most weakly granular, surface densely covered with broad pale scales near apex, the scales closed and overlapping, mostly less than three times longer than broad; **blades** ovate-cordate, subcoriaceous, shortly acuminate at apex, cordate at base, 21–22 cm long, 13–16 cm wide (1.4–1.5 times longer than wide), (0.66–0.67 as long as petiole), upper surface dark green, subvelvety and glistening, drying grayish green, lower surface much paler, semiglossy, drying yellowish brown and moderately glossy; anterior lobe 15–16.7 cm long, 15.3 cm wide (2.2–2.6 times longer than

posterior lobes); posterior lobes 6.5–6.7 cm long, 7 cm wide, rounded; sinus obovate to narrow hippocrepiform and closed; midrib drying sunken and concolorous above, convex, matte below; basal veins 6 per side, with 2 free to base, third and higher order veins coalesced 1 cm, sunken above, convex below; posterior rib not naked; primary lateral veins 3 per side, departing midrib at a 40–45° angle, quilted-sunken above, round-raised or raised, darker below; minor veins distinct, arising from both the midrib and primary lateral veins; "cross-veins" prominently raised upon drying. INFLORESCENCES probably 1 per axil; peduncle 4.5 cm long, 4 mm diam., ± terete, glabrous; **spathe** 11 cm long (2.4 times longer than peduncle), green, drying dark reddish brown; **spadix** sessile, 9.5–10.5 cm long; pistillate portion 3 cm long, 1 cm diam.; staminate portion 6.5–7.5 cm long, 1–1.5 cm diam.; pistils 1.5 mm long, 1.9 mm diam.; ovary 6-locular, 1.2 mm diam., locules 1 mm long, 0.3 mm diam., ovule sac 0.1–0.2 mm long, with axile placentation; ovules ca. 14 per locule, 2-seriate, contained within small, cloudy, gelatinous ovule sac, 0.1–0.2 mm long, longer than funicle; funicle to 0.1 mm long, adnate to lower part of partition, style similar to style type B; style apex flat; stigma hemispheroid, lobed, 1 mm diam., 0.3–0.4 mm high, covering entire style apex, depressed shallowly at center; the androecium truncate, ± prismatic, margins irregularly 4–5-sided, ca. 1 mm long; sterile staminate flowers irregularly 4–5-sided, 1.6–2.1 mm long.

Flowering in *Philodendron hammelii* apparently occurs in the early wet season, based on a single collection made in June.

Philodendron hammelii is endemic to Panama, known only from the type in Coclé Province in *Premontane rain forest* at 850 to 1100 m elevation.

Philodendron hammelii is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is characterized by its short, slender internodes; persistent, thin, pale network of branched cataphyll fibers; petioles longer than the blades and densely covered with broad, pale scales near the apex; and ovate-cordate, yellow-green-drying blades.

Philodendron hammelii is superficially most similar to *P. colombianum* R. E. Schult. from the Amazon basin. These species have similarly shaped blades drying yellow-green with prominent "cross-veins" and persistent, pale cataphyll fibers. *Philodendron colombianum* differs, however, in having the blade sinus acute at apex and petioles lacking scales.

In Panama, this species might be confused with *P. squamipetiolatum,* which also has scaly petioles. It differs in having blades with a more arcuate sinus and petioles conspicuously long-scaly throughout most of their length.

The species is named in honor of Barry Hammel of the Missouri Botanical Garden who has collected many important Araceae in Panama and Costa Rica, including the type specimen.

Philodendron hebetatum Croat, sp. nov. TYPE: Panama. Coclé: vicinity el Valle de Antón, at forested flat area near Finca Macarenita at La Mesa, 800 m, 8°36′N, 80°07′W, 6 July 1994, *Croat & Zhu 76693* (holotype, MO–4619514–15; isotypes, B, CAS, COL, CR, F, K, NY, PMA, US). Figures 33, 218–220, 225, 226.

Planta hemiepiphytica; internodia 1–4 cm longa, 1.5–2.5 cm diam.; cataphylla ad 12–35 cm longa, incostata, persistentia semi-intacta; petiolus subteres, 27–75 cm longus, 0.8–1.8 cm diam., obtuse complanatus adaxialiter, in sicco conspicue flavibrunneus; lamina anguste ovato-triangularis, cordato-sagittata basi, 24–63 cm longa, 19–44 cm lata, atriviridi supra, opace albida, hebetata infra; inflorescentia 1–5; pedunculus 4–11 cm longus, 4–11 mm diam.; spatha 11–17.5 cm longa; lamina spathae extus viridi vel albida; tubo spathae extus atriviridi aut interdum purpureo vel violaceipurpureo vel rubro aut subroseo, intus albido vel rubello vel pallide violaceipurpureo; pistilla (4)5–8-locularia; loculi (4)20–24-ovulati.

Hemiepiphytic; stem appressed-climbing; internodes short, semiglossy, 1–4 cm long, 1.5–2.5 cm diam., longer than broad, green to gray-green, drying yellow-brown; roots moderately numerous per node, drying dark brown, ridged; cataphylls 12–35 cm long, unribbed, sometimes sharply 1-ribbed near apex (sharply 2-ribbed in South America), medium green, drying light to medium brown, persisting semi-intact at upper nodes, then deciduous with large patches of yellow-brown periderm remaining intact; **petioles** 27–75 cm long, 0.8–1.8 cm diam., ± terete, obtusely flattened adaxially, spongy (in South America), dark green to gray-green, surface semiglossy to matte, transversely fissured near apex, drying pale yellow-brown. LEAVES erect-spreading; **blades** ovate-triangular, subcoriaceous, abruptly acuminate at apex, cordate-sagittate at base, 24–63 cm long, 19–44 cm wide (1.1–2.3 times longer than wide), (0.7–1.2 times longer than petiole), equal to or longer than petiole, margins concave, broadly undulate, upper surface semiglossy, dark green, drying conspicuously yellow-brown, semiglossy, lower surface opaque whitish, matte, paler; anterior lobe 19.5–49.5 cm long, 14.5–42 cm wide (1.9–3.6 times longer than posterior lobes); posterior lobes 7.1–20.2

cm long, 7.3–20.5 cm wide, obtuse to rounded; midrib broadly concave, paler than surface above, thicker than broad, weakly glossy, darker than surface below; basal veins 6 per side, with 1–2 free to base, second and third veins coalesced ca. 3 cm; posterior rib naked for 2.5–3.5 cm long; primary lateral veins 6–11 per side, departing midrib at a 35–50° angle, weakly sunken above, convex and darker than surface below; minor veins moderately distinct, fine, intermittent below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1–5 per axil; peduncle 4–11 cm long, 4–11 mm diam., white-lineate to coarsely white-streaked toward apex and on spathe base; **spathe** 11–17.5 cm long, 2–3.5 cm diam. (1.3–3.1 times longer than peduncle), white-speckled, semiglossy, constricted above the tube, 9–11 mm diam. at constriction; spathe blade green to whitish, sometimes rose-red outside, green to whitish or sometimes rose-red and white-speckled inside; spathe tube oblong-ellipsoid, 4–7 cm long, usually dark green or sometimes purple to violet-purple to red or pinkish outside, reddish to pale violet-purple (dark maroon in South America) inside; **spadix** white, cylindrical, 12.9–16.6 cm long, broadest near the base, constricted near the middle; pistillate portion whitish, cylindrical to ovoid, 3.8–8.9 cm long, 7–16 mm diam.; staminate portion 9.3–13.4 cm long; fertile staminate portion cylindrical, 8–13 mm diam., broadest at the base, narrower than pistillate and sterile portions; sterile staminate portion as broad as or narrower than the pistillate portion, 1–1.3 cm diam.; pistils glossy, 2.1–4(5.8) mm long, 1.2–2.6 mm diam.; ovary (4)5–8-locular, walls embedded with granular, crystal-like particles, locules 1.3–3.2(4.5) mm long, 0.4–0.6 mm diam., with axile placentation; ovules (4)20–24 per locule, 2-seriate, 0.2 mm long, about equal in length to funicle; funicle 0.1 mm long, adnate to lower part of axillar wall, style 0.4–0.7 mm long, 1.2–2.6 mm diam., similar to style type B; style apex flat or rounded; stigma subdiscoid, 1–1.5 mm diam., 0.2–0.5 mm high, covering center of style apex; the androecium truncate, margins 4–6-sided, sometimes scalloped; thecae oblong, 0.3–0.4 mm wide, contiguous, ± parallel to one another; sterile staminate flowers 3–6-sided, 1.5–2.5 mm long, 1.4–1.8 mm wide. Berries white, with purple stigmas; seeds 2–3, 6, 10–12, 18–25 per locule, (1–5)8–11 mm long, 2–3 mm diam.

Flowering in *Philodendron hebetatum* apparently occurs throughout the dry season and first part of the rainy season in Panama, from December through July. Post-anthesis inflorescences have been collected from January through October (except September). Immature fruits have been collected in June and July. South American collections follow more or less the same pattern as those from Panama.

Philodendron hebetatum ranges from Panama to Colombia (Chocó) and Ecuador (Carchi, Esmeraldas, and Pichincha) along the Pacific coast, at 10 to 1880 m elevation in *Premontane wet forest, Tropical wet forest,* and *Premontane rain forest* life zones. It is to be expected in adjacent Costa Rica. In Panama, most collections have been made at or less than 1400 m, rarely to about 1630 m.

Philodendron hebetatum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Impolita.* This species is characterized by its generally appressed-climbing hemiepiphytic habit; short internodes; usually unribbed, semi-intact persistent cataphylls with large patches of yellow-brown epidermis remaining intact; petioles equaling or exceeding the blade in length and drying conspicuously yellow-brown and smooth (thus clearly demarcated from the blade); and markedly bicolorous, narrowly ovate-triangular blades usually concave along the margin and matte and whitish on the lower surface.

The petioles of *P. hebetatum* are variable, being typically terete to obtusely D-shaped in Central America but sharply C-shaped to sharply D-shaped with acute to bluntly raised lateral margins in South America. South American populations also have the major leaf veins drying yellowish to pale red vs. dark red in Central America. It is possible that the South American elements may ultimately prove to be at least subspecifically distinct.

Some South American specimens of *P. hebetatum* are particularly noteworthy. *Holm-Nielsen et al. 25665,* from Ecuador, differs from other collections in having the petiole epidermis drying paler yellow and the immature spathes drying a paler reddish brown. A collection from Nariño Department, Colombia (*Croat 72425A*), is unusual in having the margins of the anterior lobe markedly concave, but perhaps belongs also to this species.

Philodendron hebetatum is easily confused, especially in live condition, with *P. thalassicum,* which may also have triangular-ovate blades much paler and matte on the lower surface. The latter differs, however, in having petioles that are sharply D-shaped and dry blackened rather than conspicuously yellow-brown. In addition, *P. hebetatum* has spathes reddish within, while in *P. thalassicum* they are greenish within.

Philodendron hebetatum is also similar to *P. strictum,* which differs by its usually terrestrial hab-

it, more or less reclining stems, and broadly ovate blades. Both species have pale, matte lower blade surfaces, yellow-brown drying petioles, and cataphylls with persistent patches of intact, yellowish brown epidermis. The lower blade surface in both species is covered with a wax-like substance, and dries with a fine reticulate pattern (areolate at 7× or higher magnification). *Philodendron strictum* ranges from Costa Rica to Panama and Venezuela at 650 to 1900 m elevation. In Panama, where both species occur together along the Fortuna Dam Road, *P. strictum* tends to occur at higher elevations than *P. hebetatum*.

Juvenile plants (*Croat 56049, 56174, 56213, 69291*; Valle and Chocó Departments, Colombia) of *P. hebetatum* have oblong-elliptic leaf blades acute at the base, but the petiolar epidermis already is colored as in adult plants. Leaves of older plants become increasingly rounder and broader at the base and finally subcordate to cordate.

An unusual collection is *Croat 49298* from Chocó Department, Colombia, with leaves only shallowly cordate, even though they are in the upper end of the size range for adult plants of this species.

Sánchez et al. 553, a collection from Colombia (Antioquia), is noteworthy in being from 1880 m elevation and in being terrestrial. *Holm-Nielsen et al. 25665* from Ecuador (Esmeraldas) differs from other South American collections in having a paler, flakier epidermis on the petioles and smaller, more or less sessile (perhaps immature) inflorescences. Perhaps it represents another species. South American collections of *P. hebetatum* differ from those of Panamanian material in that the petioles dry dark brown rather than yellowish.

Croat 61396 is unusual in apparently having only four ovules per locule.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 2.8 mi. N of Divide, 850–950 m, ca. 8°45′N, 82°15′W, *McPherson 9663* (MO, NY); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60263* (CM, MO); 13.2 mi. W of Chiriquí Grande, 310 m, 8°45′N, 82°10′W, *60140* (AAU, MO). **Chiriquí**: Cerro Colorado, 18–27 mi. off Pan-American Highway along mining road, 1200–1500 m, *Croat 33141* (MO); 1390–1410 m, *Croat 37223* (MO); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69064* (CM, MO, PMA); 8.3 mi. beyond Chame, 1630 m, *Croat 75042* (MO); *75046* (CM, MO); Fortuna Dam area, 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°07′W, *Croat & Grayum 60073* (B, CM, MO); 11.8 mi. N of Los Planes de Hornito, *Croat 48668* (MO). **Coclé**: El Copé region, 9.4 km above El Copé, 750–900 m, *Croat 44686* (CAS, MO); Alto Calvario, 800 m, 8°39′N, 80°36′W, *Croat 75075* (CM, MO); 710–800 m, 8°39′N, 80°36′W, *Croat 68712* (ENCB, MO); El Valle region, vic. of La Mesa, N of El Valle de Antón, 900–1000 m, 8°37′N, 80°08′W, *Croat 67279* (MO); 8°37′N, 80°07′W, *McPherson 11203* (CM, M, MO); 8°40′N, 80°07′W, *Knapp 5337* (MO); *5753* (MEXU, MO); La Mesa, 775 m, 8°36′N, 80°07′W, *Croat 74783* (MO, QCA); *14372* (MO); 2000–2700 ft., *Dwyer et al. 4567* (MO, NY); 860–900 m, *Croat 37364* (MO); ca. 800 m, *25407* (MO); 800–900 m, 8°38′N, 80°09′W, *67204* (DUKE, MO, US). **Darién**: Parque Nacional Darién, near gold mine at headwaters of N branch of Río Pucuro, slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, 1300–1500 m, 8°09′5″N, 77°15′W, *Hammel et al. 16541* (COL, MO); Río Tuquesa, Tyler Kittredge gold mine, ca. 2 air km from Continental Divide, *Croat 27240* (MO). **Panamá**: Cerro Jefe region, vic. of summit, 850 m, 9°14′N, 79°22′W, *Croat 67060* (MO, NY); 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76611* (CM, K, M, MEXU, MO, W); 4.6 km beyond peak on road to Alto de Pacora, 26.3 km from InterAmerican Highway, 600 m, *Croat 35934* (MO); 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above highway, 700–750 m, 9°15′N, 79°25′W, *Croat 68661* (IBE, MO); 5–10 km NE of Altos de Pacora, 700–800 m, *Mori & Kallunki 6031* (MO); El Llano–Cartí Road, Mile 10, near El Llano, 330 m, *Croat 33773* (MO, US); Cerro Campana, ca. 850 m, 8°40′N, 79°50′W, *Thompson 4598* (MO), *Croat 17243* (MO), 780–875 m, *25224* (F, MO, PMA); 1000 m, *Luteyn 3193* (DUKE); ca. 1 mi. from Inter-American Highway, ca. 150 m, *Croat 35961* (F, MO); above Su Lin Motel, *Croat 14726* (MO, PMA); lower slopes above FSU cabin, 850 m, *Croat 22795A* (MO). **San Blas**: El Llano–Cartí Road, Mile 14, 300 m, 9°15′N, 79°W, *Croat 69231* (MO, PMA, SAR); sendero de Interpretación, 1 km al este del Campamento de los guardabosques de INRENARE, 800–900 m, 8°40′N, 79°55′W, *Correa et al. 9489* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río Calovébora, 0.6 mi. beyond Escuela Agrícola Alto Piedra, 735 m, *Croat & Folsom 33996* (MO); Cerro Tute, 800–1100 m, 8°35′N, 81°5′W, *Hamilton & Krager 3934* (MO); Río Tercero Braso Valley, beyond Escuela Agrícola Alto Piedra, above Santa Fe, *Croat 27326* (MO).

COLOMBIA. **Antioquia**: Mpio. Frontino, Corregiento Nutibara, valley of the upper Río Cuevas, 1880 m, *Sánchez et al. 553* (MEDEL); Río Anorí, confluence of Quebrada La Tirana and Río Anorí, ca. 3 km upriver from Planta Providencia, 28 km SW of Zaragoza, 400–700 m, *Alverson et al. 299* (COL, WIS); Río Anorí valley near Planta Providencia, 350–600 m, 7°30′N, 74°50′W, *Shepherd 924* (COL, WIS). **Chocó**: Quibdó–Tutunendo Road, ca. 3 km W of Tutunendo, 80 m, *Gentry et al. 30108* (MO); 1 km E of Tutunendo, 100 m, 5°46′N, 76°35′W, *Gentry et al. 30079* (COL); Medellín–Quibdó, Km 136.4, 63 km E of Tutunendo, 960 m, 5°47′N, 76°22′W, *Croat 56348* (COL, JAUM, MO); Km 208.5, 9 km W of Tutunendo, <100 m, 5°39′N, 76°40′W, *Croat 56213* (MO); Río Atrato, 39 km W of Bolívar, 1600 m, *Croat 49261* (MO); 78 km W of Bolívar, 466 m, *Croat 49298* (MO); 27 mi. W of Bolívar, 1190 m, 5°50′N, 76°16′W, *Croat & Cogollo 52089* (MO); Quibdó–Bolívar, Km 137–138, 79–80 km E of Quibdó, 910–920 m, 5°45′N, 76°21′30″W, *Croat 57345* (COL, JAUM, MO); Quibdó-Las Animas, ca. 1 km N of Las Animas, ca. 100 m, 5°14′N, 76°40′W, *Croat 55958* (COL, MO); San José del Palmar–Cartago, Vereda La Bella between San José del Palmar and turnoff to El Cairo, 1430 m, 4°53′N, 76°13′W, *Croat 56715* (COL, MO, QCA); Pueblo Rico (Risaralda)–Istmina (Chocó), Quebrada Antón, 15 km W of Santa Cecilia, 6 km W of Chocó–Risaralda border, 240–350 m, 5°20′30″N, 76°13′45″W, *Croat 70961* (MO); Quibdó–Istmina, Km 4, <100 m, 6°28′N,

76°36′W, *Croat & Cogollo 52234* (MO); Serranía de Baudo, Las Animas–Pato on Río Pato, ca. 150 m, 5°30′N, 76°46′W, *Croat 56131* (COL, JAUM, MO, PMA); 16 km NW of junction with Quibdó–Istmina road near Las Animas, 100 m, 5°20′N, 76°42′W, *Croat 56174* (COL, JAUM, MO); 5°16′N, 76°41′W, *Croat 56049* (COL, JAUM, MO); Río San Juan, Docordó, 0 m, 4°15′N, 77°22′W, *Forero et al. 4352* (MO). **Nariño**: along road between Junín and Barbacoas, 1.9 km NE of Junín, 1130 m, 1°21′N, 87°6′W, *Croat 72425A* (CM, MO). **Risaralda**: Mpio. Mistrato, Chirrincha, Río Aguita, 950 m, *Franco et al. 3522* (MO); corregimientos de Geguadas–Puerto de Oro, 1550 m, *Alonso et al. 9819* (MO); *9742* (MO). **Valle**: Bajo Calima area, *Croat 62761* (CM, MO); ca. 15 km N of Buenaventura, Cartón de Colombia concession, Juanchaco region, 500 m, 3°56′N, 77°08′W, *Gentry et al. 53711* (MO); Lijal–Gasolina road junction, SSW of San Isidro, 50 m, *Gentry et al. 62926* (MO); 11 km N of main Cali–Buenaventura Highway, ca. 50 m, 3°56′30″N, 77°01′W, *Croat & Monsalve 61396* (MO, QCA); Buenaventura–Río Calima, 33.3 km N of Cali–Buenaventura Highway, ca. 50 m, 4°02′N, 77°07′W, *Croat 61279* (COL, MO, NY, TEX); Km 11, 50–80 m, 3°56′30″N, 77°01′W, *Croat 69291* (CAS, F, L, MO, US); ca. 4 km from Río Calima, near Km 14 marker, <50 m, 3°56′N, 76°59′W, *Croat 57530* (AAU, DUKE, K, MEXU, MO); Buenaventura–Málaga Road, 185 m, 3°56′N, 77°01′W, *Croat 70103* (B, CAS, COL, F, K, MO, PMA, US); km 17.5, 130 m, 3°57′N, 77°01′W, *Croat & Bay 75629* (MO); Km 18–20 on Cali–Buenaventura Highway, Finca Zingara, 1500–2000 m, *Cabrera & van der Werff 15779* (MO); Río Cajambre, 5–80 m, *Cuatrecasas 17054* (US); Río Naya, upriver from Puerto Merizalde, ca. 10 m, 3°15′N, 77°25′W, *Gentry & Juncosa 40673* (MO). ECUADOR. **Carchi**: Tulcán Cantón, Reserva Indígena Awá, sector Sabalera, parroquia Tobar Donoso, 650–100 m, 1°N, 78°24′W, *Tipaz et al. 1298* (MO); *1462* (MO). **Esmeraldas**: Lita–San Lorenzo, 15.5 km W of Lita, 705 m, 0°55′N, 78°28′W, *Croat 72372* (MO); San José de Cayapas, 80 m, 0°52′N, 78°57′W, *Holm-Nielsen et al. 25665* (AAU, MO); Eloy Alfaro, Reserva Ecológica Cotacachi–Cayapas, Charco Vicente, Río San Miguel, afluente del Río Cayapas, 150 m, 0°43′N, 78°53′W, *Palacios & Tirado 11276* (MO, QCNE). **Pichincha**: Reserva ENDESA, Quito–Puerto Quito, Km 113, 0°05′N, 79°02′W, 750 m, *Croat & Rodríguez 61454* (CM, K, M, MO, QCA); *61455* (K, MO, QCA); 710 m, 0°03′N, 79°07′W, *Croat 73155* (AAU, B, COL, F, K, MO, NY, QCA, US).

Philodendron hederaceum (Jacq.) Schott, Wiener Z. Kunst. 1829: 780. 1829. *Arum hederaceum* Jacq., Enum. Syst. Pl. 31. 1760. TYPE: t. 51, fig. D in Plum., Pl. Amer., 1756 (holotype). Figures 221–223.

Hemiepiphytic vine; growing to often high in trees, stem appressed-climbing, eventually scandent, often pendent, sap clear, turning honey-colored, leaf scars 7–15 mm long; internodes weakly flattened on one side, sometimes with 2 sharply raised on the side above the petioles, usually weakly glossy, sometimes matte, pale to medium green, minutely speckled to striate, usually smooth when fresh, but drying minutely ridged, sometimes prominently ribbed throughout its circumference (the ribs smooth to prominently warty), (2)10–28 cm long, 1–2.5(3.5) cm diam., dark green, usually drying green, sometimes reddish; roots brown, to 10 cm long, many at nodes; cataphylls 6–10 cm long, unribbed, weakly 1-ribbed, or bluntly to sharply 2-ribbed, pale green, deciduous; **petioles** (6)9.7–27(33) cm long, 6–10 mm diam., terete to subterete, pale green, firm, flattened adaxially, pale green, surface smooth, weakly glossy to matte; **blades** broadly ovate, subcoriaceous to coriaceous, semiglossy to matte, acuminate to long acuminate, sometimes cuspidate at apex (the acumen inrolled, 0.5–0.9 mm long), 11–40(50) cm long, 8–24(34) cm wide (1.2–1.9 times longer than wide), (ca. 1.3(1.5) times longer than petiole), margins hyaline to pale yellowish, upper surface dark green, sometimes subvelvety, lower surface slightly paler, often purplish violet, drying gray-green to yellow-green; anterior lobe 9–30(41) cm long, 9–24(29) cm wide ((2)2.4–3.7(6.3) times longer than posterior lobes); posterior lobes 3–10(14) cm long, 4.3–15.7 cm wide, directed inward and sometimes overlapped, obtuse to rounded; sinus usually deeper than broad, mostly spathulate, rarely hippocrepiform, 3–7 cm deep; midrib convex to flat or sunken, concolorous or slightly paler than surface above, convex, concolorous below; basal veins (3)4–5(6) per side, with (0)1–2 free to base, part of the remainder coalesced to 1.5–2 cm; posterior rib not naked; primary lateral veins 2–6 per side, departing midrib at a 35–55° angle, ± straight to the margins, sunken to weakly raised, slightly paler than surface above, convex and paler than surface below; minor veins obscured to moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES erect or pendent, 1 per axil; peduncle (2–3)4–15.7 cm long, 8–12 mm diam., pale green, sometimes tinged purple, matte; **spathe** subcoriaceous to coriaceous, 9–16.6(24) cm long, (0.9–2.6(3.3) times longer than peduncle), weakly constricted above the tube, 1.3–3.6(5.7) cm diam. at constriction, usually green, sometimes yellowish white, yellowish green, or cream to creamy-white throughout; spathe blade sometimes purple tinged outside, 1.2–3.6 cm diam. when furled, pale green, greenish yellow, sometimes tinged red inside; spathe tube dark green, sometimes tinged reddish maroon outside, 5–6 cm long, 1.5–4.9(6.9) cm diam., maroon, dark red, crimson, or purple at base inside; **spadix** stipitate to 5–10 mm long, dark maroon; 12–20 cm long; pistillate portion pale greenish white to green, 3.5–6 cm long, 1.5 cm diam. at base, 1.7 cm diam. at middle and near apex; staminate portion 7–11 cm long; fertile staminate portion creamy white to pinkish, broadest at base,

weakly constricted ca. 1 cm above sterile portion then ± uniform to near apex, 1.4–2.2 cm diam. at middle, 9 mm diam. ca. 1 cm from apex; sterile staminate portion 1.6 cm diam.; pistils 4–9.2 mm long, 1.8–3.1 mm diam.; ovary 4–6(7)-locular, 8 mm long, locules 8 mm long, 1.4 mm diam., with axile placentation; ovules 20–25 per locule, 0.1 mm long, 2-seriate; funicle 0.1–0.3 mm long, adnate to lower part of partition, style 1.1 mm long, 2.9 mm diam., similar to style type B; style apex flat or somewhat rounded, drying concave with a pale margin and 4–6 paler, flat to weakly sunken circular areas associated with the stylar pores; stigma 3–4-sided, light brown to reddish, drying light brown, 1.8–3.3 mm diam., 0.35 mm high, margins thin; sterile staminate flowers blunt, irregularly 4–5-sided, 2.2 mm long, 1.3 mm wide. INFRUCTESCENCE pendent, often on leafless stems; spathe dark green, weakly glossy outside; pistillate spadix 5–8 cm long, 3.5–4 cm diam.; berries greenish white; seeds 1–2 per locule, somewhat orange, many per berry, ± ovoid to oblong ellipsoid, (1.5)3–5 mm long, 2.5–4 mm diam., with weak constriction (nipple) and densely covered with raphide cells. JUVENILE plants with upper blade surface dark green, sometimes reddish green, with glistening minute close papillations, lower surface somewhat maroon; veins less conspicuous.

Philodendron hederaceum ranges throughout the West Indies and from Mexico throughout Central America and much of South America, at sea level to 1200(1500) m elevation. In South America it extends from as far south as Los Ríos Province in coastal Ecuador to Trinidad, Venezuela, the Guianas, Brazil, Ecuador, Peru, and Bolivia on the Atlantic drainage of the continent.

Philodendron hederaceum is a member of *P.* sect. *Philodendron* subsect. *Solenosterigma.* This species is distinguished by its scandent habit, long internodes, deciduous cataphylls, ovate-cordate, long-petiolate leaves, and solitary inflorescence with usually green spathes with the tube reddish to purplish within.

Philodendron hederaceum is most easily confused with *P. purpureoviride,* which is a vine with similar leaves. See that species for differences.

Philodendron hederaceum is also somewhat similar to *P. jacquinii,* but the latter differs in its generally pubescent stems, petioles and major veins of the lower blade surface, its thinner leaf blades, swollen spathe tube, and broad pistillate portion of the spadix with elongate styles.

The taxa here treated as *Philodendron hederaceum* and *P. jacquinii* have long been confused nomenclaturally. The former name is based on *Arum hederaceum,* first validly published by N. J. Jacquin (1760) in his *Enumeratio Systematica Plantarum.* Jacquin cited only a Plumier (1756) plate (t. 51, fig. d), which thus must be accepted as the holotype of the name (Greuter et al., 1994; Art. 9.1, Note 1). Three years later, Jacquin (1763), in his *Selectarum Stirpium Americanarum Historia,* published his own plate (t. 152), identified as *A. hederaceum* but actually depicting a different species from Cartagena, Colombia, namely, that treated in this revision as *P. jacquinii* Schott. These two species are fortunately sufficiently different in appearance that even drawings of sterile plants, such as that of Plumier, are unmistakable. This mistake by Jacquin has caused considerable confusion, since several authors, including Kunth (1841), Engler (1899), Krause (1913), Dugand (1945), and Bunting (1963b, 1995), have misapplied the name *P. hederaceum* based on Jacquin's (1763) publication.

Schott, however, understood the problem. He had already transferred *Arum hederaceum* to *Philodendron* (Schott, 1829), and in his treatment for *Synopsis Aroidearum* (Schott, 1856) he described *P. jacquinii,* explicitly basing it on Jacquin's (1763) plate. Schott (1856) also placed *P. hederaceum* sensu Kunth into synonymy under his newly described *P. jacquinii.* However, he included *P. hederaceum* in his grex *Macrobelium,* while treating other synonyms of *P. hederaceum* in grex *Solenosterigma.* Names so treated were: *P. scandens, P. prieurianum, P. oxycardium, P. cuspidatum,* and *P. micans.*

Engler (1899), followed by Krause (1913), treated the species herein called *P. hederaceum* as four distinct species: *P. prieurianum, P. scandens, P. oxycardium,* and *P. micans.* Both Engler and Krause erred in treating *Arum hederaceum* Jacq. as a questionable synonym of *P. hoffmannii* (= *P. jacquinii*), citing Jacquin's (1763) t. 152 as the type.

Despite the confusion by Engler and Krause, Standley and Steyermark (1958b) correctly dealt with the taxonomy of *P. hederaceum,* citing *P. scandens, P. oxycardium,* and *P. miduhoi* in synonymy. Their treatment of *P. jacquinii* was incorrect, since they cited that name under the later synonym *P. hoffmannii* Schott (1858). In this regard they followed Krause (1913). Thus, despite the confusion by Engler and by Krause, the nomenclature of these species was essentially rectified as early as 1958 to the species as *P. oxycardium* or *P. cordatum* hort. (non Vell.).

Bunting (1963b), apparently following the lead of Dugand (1945), was aware of the Plumier illustration cited by Jacquin but seemed to believe that it had no bearing on the application of the name.

He also referred to Jacquin (1763) as the "initial" publication of *Arum hederaceum*, presumably in the erroneous belief that the name had not been validly published in Jacquin (1760). Bunting (1963a) accordingly applied the name *P. hederaceum* to the species here called *P. jacquinii* and the obscure *P. scandens* K. Koch (1853) for the species herein called *P. hederaceum*. Certainly the epithet *P. scandens* was not in general use up until that time because most horticultural works (Birdsey, 1951) still referred to the species as *P. oxycardium* Schott.

Other, more practical matters substantiate that Plumier's (1756) rather crude drawing depicts the species here treated as *P. hederaceum*, rather than the one called *P. jacquinii* (accurately illustrated by Jacquin, 1763). Plumier's text associated with t. 51, fig. D states that the plant grew in Martinique, known to have been visited by Plumier (Urban, 1898: 123). *Philodendron hederaceum* is a widespread species in the West Indies and occurs on Martinique, while *P. jacquinii*, though also widespread, is not known from the Lesser Antilles. The epithet *hederaceum* connotes an ivy-like growth habit and aspect, apt for the species to which the epithet is here applied, but not for *P. jacquinii*. The application of the name *P. hederaceum*, as explained above, is unambiguous, whereas that of *P. scandens*, the name used during the last 30 years for this plant, is highly dubious, as it is based on a sterile Koch specimen of unknown origin, lacking an extant type specimen or even illustrations.

Article 57.1 of the Tokyo Code (Greuter et al., 1994) states that "A name that has been widely and persistently used for a taxon or taxa not including its type is not to be used in a sense that conflicts with current usage unless and until a proposal to deal with it under Art. 14.1 or 56.1 has been submitted and rejected." I consider that this Article does not apply in the present case, since the name *P. hederaceum* was used in the sense, including its type, as recently as 1958, in a higher regional flora (*Flora of Guatemala*), which is the most recently published treatment of Araceae for any Central American country and still reigns as the standard work throughout the region.

In Central America, *P. hederaceum* can be divided into three varieties. *Philodendron hederaceum* var. *hederaceum* and *P. hederaceum* var. *oxycardium* (Schott) Croat are only distinguishable on the basis of their juvenile leaf blades. In *P. hederaceum* var. *hederaceum*, the juvenile blades are velvety with a silky sheen on the upper surface, whereas the juvenile blades of *P. hederaceum* var. *oxycardium* are glossy on the upper surface. These juvenile forms were formally treated by Bunting (1968) as *P. scandens* forma *micans*.

The third newly recognized variety, *P. hederaceum* var. *kirkbridei* Croat, is distinguishable by its adult stems that dry brown and are deeply sulcate with prominent ridges. This taxon also differs in occurring at higher elevations.

The following key separates the three varieties of *P. hederaceum* in Central America. For anatomical differences see Bunting (1968).

KEY TO THE VARIETIES OF *P. HEDERACEUM*

1a. Adult stems weakly sulcate on living plants, moderately to conspicuously sulcate and reddish brown upon drying, usually densely warty; spathe tube dark red to red-purple inside; Costa Rica, Panama, Ecuador, and Suriname, mostly 450–900 m elevation ..... var. *kirkbridei*

1b. Adult stems smooth, drying mostly green, weakly striate, never minutely warty; spathe tube green (sometimes weakly tinged reddish) inside.

2a. Juvenile blades velvety with a lustrous sheen on the upper surface, often tinged purplish on the lower surface; apparently ranging throughout the range of the species in Mexico, Central America, and to the West Indies and South America (including Amazonian basin) ..... var. *hederaceum*

2b. Juvenile blades glossy on the upper surface, green on the lower surface; known only from the Gulf slope of Mexico in Veracruz, northern Oaxaca, and Tabasco, but possibly also found in Jamaica ..... var. *oxycardium*

Philodendron hederaceum (Jacq.) Schott var. **hederaceum**

Philodendron scandens K. Koch & Sello, in A. Braun et al., Append. sp. Hort. berol. 1853: 14. 1853–1854. TYPE: A cultivated plant grown in Berlin, origin not stated (holotype, B lost).

Philodendron harlowii I. M. Johnst., Sargentia 8: 91, t. 14, fig. 1. 1949. TYPE: Panama. Panamá: San José Island, area 11B, *Johnston 1030* (holotype, GH; isotype, MO).

Philodendron miduhoi Matuda, Revista Soc. Mex. Hist. Nat. 11: 95, figs. 6–7. 1950. TYPE: Mexico. Chiapas: Finca Esperanza, 160 m, 23 Dec. 1949, *Matuda 18721* (holotype, MEXU; isotype, UC).

Philodendron cuspidatum K. Koch & Bouché, in A. Braun et al., Append. Gen. sp. Hort. berol. 1854: 7. 1854–1850. *Philodendron scandens* var. *cuspidatum* (K. Koch & Bouché) Engl., Bot. Jahrb. Syst. 26: 528. 1899. TYPE: cultivated at Berlin Botanical Garden (holotype, B? destroyed). Schott ic. 2679 (neotype, here designated).

Philodendron micans K. Koch, in A. Braun et al., Append. Gen. sp. Hort. berol. 1854: 7. 1854–1855. *Philodendron scandens* f. *micans* (K. Koch) G. S. Bunting, Gentes Herb. 10: 63. 1968. TYPE: original locality unknown (holotype, B? destroyed). Schott ic. 2709 (neotype, here designated, W).

Philodendron microphyllum K. Koch, in A. Braun et al., Append. Gen. sp. Hort. berol. 1854: 7. 1854–1855. TYPE: cultivated collection at Berlin (holotype, B? now lost).

Philodendron oxyprorum Schott, Syn. Aroid. 82. 1856. TYPE: Venezuela. [Synonymized by Engler (1899) but no specimen or illustration now exists.]

Philodendron acrocardium Schott, Oesterr. Bot. Z. 8: 179. 1858. TYPE: Guatemala, *Wendland* (holotype, W? destroyed). Schott ic. 2498 (neotype, here designated).

Philodendron pittieri Engl., Bot. Jahrb. Syst. 26: 541. 1899. TYPE: Costa Rica. Puntarenas: Ujarrás de Buenos Aires, 9°12′N, 83°17′W, Feb. 1897, *Pittier 11132* (holotype, B; isotype, BR).

Hemiepiphyte; internodes 10–25 cm long, 1–2.5(3.5) cm diam., weakly flattened on one side, medium green, minutely speckled to striate or smooth when fresh but drying minutely ridged, greenish; cataphylls 6–10 cm long, unribbed, weakly 1-ribbed or bluntly to sharply 2-ribbed, deciduous intact; **petioles** (6)10–27(33) cm long, 6–10 mm diam.; blades (11)16–40(50) cm long, 8–24(34) cm wide; upper surface medium to dark green, velvety when juvenile, drying brown to greenish brown, lower surface medium green, glossy, drying gray-green to yellow-green; primary lateral veins 2–6 per side, departing midrib at a 35–55° angle. INFLORESCENCES with peduncle (2)4–16 cm long; **spathe** 9–17(20) cm long, spathe usually green, sometimes yellowish white, spathe blade sometimes tinged purple outside; spathe tube dark, sometimes tinged reddish maroon outside; **spadix** stipitate to 5 mm, 12–18 cm long; ovary 4–6-locular, 20–25 ovules per locule. INFRUCTESCENCES with many seeds per locule.

Flowering in *Philodendron hederaceum* var. *hederaceum* is rare (known only in October and November), although the species has been found in pre-anthesis condition in every month of the year. Post-anthesis collections predominate in the dry season and earliest part of the rainy season from December through May, but there are a surprisingly large number of post-anthesis collections made in November, a month when very little flowering generally takes place (Croat, 1975, 1978). Mature fruiting collections have been made from April and May, also indicating that the species may flower predominantly in the dry season.

The range of *P. hederaceum* var. *hederaceum* is essentially that of the species. It is the most widespread taxon of *Philodendron* and, indeed, perhaps of all neotropical Araceae, ranging from San Luis Potosí State in Mexico to the Greater and Lesser Antilles, and down both slopes of the Andes, east to the Guianas and south to Brazil and Bolivia. In Central America, the variety occurs on both slopes of the Continental Divide. In Mexico, it ranges from sea level to 1200(1500) m elevation, whereas in Middle America and Panama it ranges mostly to 450 (rarely to 900) m. It occurs principally in *Tropical moist forest* but ranges into *Premontane wet forest* and even *Tropical wet forest*. A single sterile pre-adult collection from *Tropical wet forest* transition to *Premontane wet forest* in Bajo Calima (*Bay 237*) is apparently also this species.

Additional specimens examined for P. hederaceum *var.* hederaceum. BELIZE. *Gentle 617A* (MICH). **Cayo**: S of Guacamallo Bridge, *Whitefoord 2837* (BM); Millionario–Grano de Oro, 1700 ft., *Croat 23697* (MO); 0–10 mi. S on Hummingbird Highway, Belmopan, *Dwyer 12718* (MO); Río Frío, 1.5 mi. W of Augustine, 450 m, *Sutton et al. 205* (BM); 0.9 km before Caracol, 16°46′N, 89°07′W, *Balick et al. 3149* (MO). **Stann Creek**: Cockscomb Basin, Jaguar Preserve, 10 km W of Maya Center, off Southern Highway, 400 m, 16°45′N, 88°35′W, *Balick et al. 2603* (MO). **Toledo**: along highway to Punta Gorda, 1 mi. E of road to San Antonio, ca. 100 ft., *Croat 24511* (MO); Union Camp, 750 m, *Whitefoord 1773* (BM, MO); Columbia River Forest Reserve, Gloria Camp, *Holst 4422* (MO); Southern Maya Mountains, Bladen Nature Reserve, 16°29′31″N, 88°54′37″W, *Davidse & Meadows 35763* (MO). COSTA RICA. *Monell s.n.* (MO); *Tonduz 13322* (G); 800 m, *Rojas 178* (MO). **Alajuela**: Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36320* (MO); Escuela Centroameriana de Ganadería, (near Atenas), 425 m, 9°58′N, 84°22′W, *Thompson & Rawlins 1256* (CM). **Guanacaste**: Tilarán, 500–650 m, *Standley & Valerio 44563* (US); *44162* (US); *44984* (US); *46563* (US); 7 km N of Cañas, *Janzen T-24* (MO); Quebrada Desprendimiento–Quebrada Sanguijuela, along Río Las Flores, ca. 450 m, 10°40′N, 85°04′5″W, *Grayum et al. 4912* (B, CAS, CR, K, MO, US); Nandayure, Península de Nicoya, 120 m, *A. Rodriguez & Estrada 141* (CR, INB). **Heredia**: La Selva Field Station, ca. 100 m, *McDowell 810* (MO); ca. 100 m; *852* (MO); *Grayum 2565* (MO). **Limón**: 20 mi. SE of Limón, road to Punta Cahiuta, near sea level, *Croat 43174* (MO); ca. 1 km N of Shiroles, ca. 50 m, *Croat 43278* (MO); Siquirres–Río Pacuare, S of Río Pacuare, 50–100 m, 10°5′N, 83°29′W, *Burger & Liesner 6953* (MO, NY); La Bomba–Cahuita, 20 m, *Gómez & Hampshire 20129* (MO); Limón–Bomba, 0–50 m, *Taylor & Skotak 4443* (DUKE); near Carmen Station on Indiana Branch, 30 m, *Standley & Valerio 48392* (US); Parque Nacional Bahía de Portete, 0–10 m, 10°N, 83°05′W, *Thompson & Rawlins 1178* (CM); Río Jiménez, S of Guápiles, 10°17′N, 83°44′W, *Barringer 2393* (CR, MO). **Puntarenas**: Cantón de Buenos Aires, along Río Ceibo, Ujarrás, 500 m, 9°14′N, 83°18′W, *Grayum 10229* (CR, IBN, K, MO, US); Golfito, 20–200 m, 8°38′N, 83°11′15″W, *H. Schmidt 603* (CR, MO); San Vito, *Benzecry CR.CB.7C.109* (CR); Monteverde, Cordillera de Tilarán, 1500–1620 m, *Pounds 94* (MO); Cantón de Turrubares, along Río del Sur, between Río Carara and Quebrada Cimarruda, 130–150 m, 9°46′30″N, 84°32′W, *Grayum 10420* (CR, MO). EL SALVADOR. **Ahuachapán**: San Francisco Menéndez–Tacuba, 1–3 mi. above road to Río Clara Sucia, 1000–1250 m, *Croat 42135* (MO). **San Miguel**: ca. 50 mi. NW of San Miguel, along highway CA-1, *Croat 32799* (MO). **San Salvador**: vic. of Tonacatepeque, *Standley 19533* (GH, NY, US). **Sonsonate**:

Pedregal de San Isidro, ca. 3 mi. S of Lake Coatepeque, ca. 850 m, *Croat 42241* (MO). GUATEMALA. Los Amates, *Kellerman s.n.* (US); *Watson 427* (GH). **Alta Verapaz**: road to El Estor (Lago Izabal), 7 mi. E of Highway CA-14 to Cobán, 1000 m, *Croat 41480* (MO). **Escuintla**: Santa Lucia, 1045 ft., *Kellerman 4547* (US); *5285* (US). **Izabal**: Montaña del Mico, between Milla 49.5 and ridge 6 mi. from Izabal, 65–600 m, *Steyermark 38486* (F); ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41811* (MO). **Quezaltenango**: CA-2 between Coatepeque and turnoff to Colombia, 1.9 mi. W of turnoff, 580 m, 14°41′N, 91°48′W, *Croat 63394* (B, BM, MO, US). **San Marcos**: near San Rafael, 600 m, *Croat 40769* (MO). **Suchitepéquez**: 1 mi. E of Mazatenango, <500 m, *Croat 43757* (MO). HONDURAS. **Atlántida**: Lancetilla Valley, Tonacatepeque, *Pfeifer 2130* (BH, US); San José de Texíguat–El Chorizo, 100 m, *Nelson 10565* (TEFH); 4 km S of Tela, 0–100 m, *Irias 190* (TEFH, UNAH); ca. 10 mi. SE of Tela, along Río Lancetilla, 10–150 m, *Croat 42639* (MO); Quebrada Grande, ca. 10 km SW of La Ceiba, 80–140 m, 15°42′N, 86°51′W, *Liesner 26335* (MO). **Colón**: Río Selen, 7 km E of Trujillo, Howler Site, *Saunders 192* (MO). **Comayagua**: junction Río Yure–Río Humuya, 200 m, *Nelson et al. 6182* (MO). **Copán**: 13 mi. E of Copán, road to La Entrada, 750 m, *Croat 42529* (MO); Sta. Rita village, 650 m, *Molina 33668* (MO). **Cortés**: Puerto Cortés–Guatemalan border, 2–3 mi. SW of Omoa, sea level, *Croat 42555* (MO); N of Lago de Yojoa, 2–6 mi. from highway, 600 m, *Croat 42739* (MO). **Gracias a Dios**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9316* (UNAH); *9292* (TEFH, UNAH). **Olancho**: Mpio. San Estebán, near Santa María del Carbón, 21 mi. NE of San Estebán, along road to Bonito Oriental, 440 m, 15°25′25″N, 85°34′45″W, *Davidse et al. 35571* (MO; Río Guyape, San Pedro de Catacamas–Poncaya, *Blackmore & Heath 1984* (BM); Río Wampú, 8 km S of Pisijire, 500–700 m, 15°15′N, 85°25′W, *Nelson & Clewell 594* (FSU, MO). MEXICO. **Chiapas**: El Triunfo, ca. 10 mi. NE of Escuintla, 300 m, *Croat 43859* (MO); 2 mi. SW of Guatemalan border, Highway 200 to Tapachula, 300 m, *Croat 43771* (MO); Bonampak, near ruins, 500 m, *Matuda 38715* (MO); Mpio. Ocosingo, 5 km SW of Santo Domingo, 600 m, *Davidse et al. 20425* (MO); Esperanza, Escuintla, 150 m, *Matuda 17789* (NY); 6 mi. N of Ocozocoautla, 1000 m, *Croat 40584* (MO); Palenque–Bonampak, 60 mi. SE of Palenque, ca. 400 m, *Croat 40167* (MO); Palenque–Ocosingo, Highway 199, 27 mi. SW of Palenque, 210 m, *Croat 40302* (MO); Cerro Vernal, NW side, 25–30 km SE of Tonalá, 400–600 m, *Breedlove 25617* (DS). **Guerrero**: Tierra Colorada–Xalpatlahuac, Tierra Colorada, Río Comitlán, 900–1000 m, *Croat 45755* (MO); Pinotepa Nacional–Tlaxiaco, Highway 125, ca. 8.4 mi. S of Putla de Guerrero, ca. 1000 m, *Croat 45807* (MO); Tierra Colorada–Acapulco, kms 366–367, ca. 380 m, *Moore & Bunting 8840* (BH). **Jalisco**: Puerto Vallarta, 100 m, *Mexía 1314* (UC); 24.1 mi. from Autlán, ca. 300 m, *Moore & Bunting 8737* (BH); Quimixto, *Mexía 1201* (BM, CAS, DS, G, GH, MO, NY, UC, US). **Nayarit**: Miramar, ca. 10 km W of Jalcocotán, *Dressler & Wirth 2703* (US); Singaita, *Lewis s.n.* (BH); *Philbrick 785* (BH); San Blas, *Lewis s.n.* (BH). **Oaxaca**: Pinotepa–Tlaxiaco, Highway 125, 4.4 km S of Putla de Guerrero, 850 m, *Croat 45835* (MO); 12 km from Hwy. 200, road to Chayuco, 220 m, *Miller & Tenorio L. 524* (MO); Tuxtepec, Rincón del Tigre, Mpio. Acatlán, 2 km from Acatlán on road to Capilla, ca. 100 m, ca. 18°31′N, 96°36′W, *Gereau et al. 2190* (CAS, MO, RSA); Tuxtepec–Oaxaca, 10 mi. S of Valle Nacional, 700 m, *Croat 39802* (MO); 0.5 mi. S of Valle Nacional, 120 m, *Croat 39694* (MO); Esmeralda–Río Verde, Uxpanapa region, 1.1 mi. S of Esmeralda, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63233* (MO). **Puebla**: Teziutlán–Nautla, Rancho Las Margaritas, Hueytamalco, near border with Veracruz, 19°57′N, 97°16′W, *Conradt 218* (MEXU). **San Luis Potosí**: 6 mi. NW of Tamazunchale, 250 m, *Croat 39271* (MO); Tamazunchale, *Lundell & Lundell 7115* (CM); 6.5 mi. S of Matlapa, Ixtiamel, 325 m, 21°18′N, 98°47′W, *Thompson et al. 1320* (CM); *1321* (CM). **Tabasco**: Tacotalpa, *Cowan 1999* (MO). **Veracruz**: 927 m, *Birdsey 226* (UC); Huatusco–Puente Nacional, El Mirador, 21 km E of Huatusco at km 45, ca. 1200 m, *Croat 44014* (MO); near Fortín, Cervecería Moctezuma, 1000–1150 m, *Croat 39408* (MO); Mpio. Nautla, Cuatro Caminos, near Cerro Chico, 30 m, *Ventura 3600* (DS); Mpio. San Andrés Tuxtla, Estación de Biología Tropical Los Tuxtlas, LOTE 71, 400 m, *Ibarra & Colin 3126* (MO), 400 m, 18°34–36′N, 95°04–09′W, *Manríquez & Colin 3126* (MO). NICARAGUA. **Boaco**: along Hwy. 33 from Río Quilan, ca. 300–310 m, 12°35′N, 85°32′W, *Stevens 9335* (MO); Cerro Mombachito, 500–900 m, ca. 12°24–25′N, 85°32–33′W, *Stevens & Grijalva 14749* (MO); Quebrada Río Grande, NE del Cerro Mombachito, 600–700 m, 12°25′N, 85°32′W, *Moreno 354* (MO). **Chinandega**: Río Chiquito, El Viejo, 0–100 m, *Atwood 2635* (MO). **Chontales**: Río Bizcocho–Río El Jordán, 350–550 m, ca. 12°12–16′N, 85°15–17′W, *Stevens & Montiel 22589* (MO); ca. 2.8 km N of Cuapa, 400–500 m, ca. 12°17′N, 85°23′W, *Stevens 3696* (MO); 3 km N of Santo Tomás, 280–300 m, 12°05′N, 85°07′W, *Moreno 16066* (MO); Juigalpa, La Libertad, Río El Bizcocho, ca. 17.4 km NE of Río Mayales, 350–400 m, ca. 12°12′N, 85°17′W, *Stevens 4090* (BM, MO); 4 km NW of Villa Sandino, 100 m, *Davidse et al. 30786* (MO). **Managua**: ca. 4 km from Highway 12, near bridge of Río La Aduana, 80–100 m, ca. 12°02′N, 86°31′W, *Stevens 5394* (BM, LL, MO); Highway 8, ca. 2.4 km SW of intersection with Hwy. 2, km 28, ca. 700 m, 11°57′N, 86°20′W, *Stevens 3990* (MO); 4 km from Highway 8 to Highway 2 intersection, 800–860 m, 11°58′N, 86°18–19′W, *Stevens 4539* (MO); Escuela Nacional de Agricultura and Ganadería, Route 1, 12 km E of Managua, *Atwood 2930* (MO). **Matagalpa**: Matagalpa–Jinotega, km 140, ca. 900–1000 m, *Guzmán et al. 229* (MO); Cerro Musún, ca. 300 m, ca. 12°55′N, 85°16′W, *Stevens 12032* (MO); Quebrada Malacal, Hacienda La Bonanza, ca. 20 km from Matagalpa, 560 m, 13°01′N, 85°47′W, *Castro 2391* (MO). **Nueva Segovia**: 7 km SE de Santa Clara, 600–700 m, 13°40′N, 86°14′W, *Araquistain & Moreno 2191* (HNMN, LE, MO); El Terrero, 4 kms NE of El Jícaro, 500–600 m, 13°45′N, 86°07′W, *Stevens & Moreno 2215* (MO). **Río San Juan**: Río Indio, San Juan del Norte, 2 m, *Araquistain 3312* (K, M, MBM, MEXU, MO). **Rivas**: Volcán Concepción, La Esperanza, 200–400 m, 11°31′N, 85°37′W, *Robleto 1618* (ENCB, MO); Isla Ometepe, 140–350 m, 11°33–34′N, 85°36′W, *Robleto 997* (MO); SE of "La Flor," 300–800 m, 11°32–34′N, 85°37–38′W, *Robleto 1915* (MO); 400–460 m, 11°33′N, 85°37′W, *Sandino 503* (MO). **Zelaya**: road to Mina Nueva America, ca. 10 km from main road, *Stevens 12672* (MO); Ibo Tingni, N of road between Puerto Cabezas and Río Wawa, <10 m, ca. 14°9–11′N, 83°29–31′W, *Stevens 10663* (CM, MO); Puerto Cabezas, 0–20 m, 14°01′N, 83°22–23′W, *Stevens 10684* (MO); Río Blanco–Río Copalar, ca. 29 km E of Río Blanco, 200–400 m, ca. 12°50–55′N, 85°0–05′W, *Stevens 12179* (MO); "Las Mercedes," 160–180 m, *Vincelli 331A* (MO); Matagalpa–Waslala, near Río Las Carpas and Río Babasca, 540–580 m,

13°15′N, 85°32′W, *Sandino 2426* (MEXU, MO); La Luz, ca. 200 m, 13°44′N, 84°47′W, *Ortiz 1606* (F, MO); Cerro Waylawás, E side of Central Range, ca. 100–200 m, 13°38–39′N, 84°48–49′W, *Pipoly 4172* (MO); 6 km SE of Waslala, 520–560 m, 13°16′N, 85°24′W, *Moreno 17279* (MO); Estación Experimental "El Recreo," ca. 15 m, 12°09′N, 84°17′W, *Rios 176* (MO); ca. 80 m, 13°39′N, 84°48′W, *Pipoly 4450* (MO); Río Prinzapolka–Quebrada San Rafael, Waní, ca. 100 m, ca. 13°42′N, 84°50′W, *Pipoly 4593* (MO); ca. 0–100 m, ca. 13°42′N, 84°50′W, *4739* (MO); Río Waní, Boca de Waspuke, 90–100 m, ca. 13°44′N, 84°53′W, *Stevens 7195* (MO); Rama, *Atwood & Moore 897* (MO); Caño Monte Cristo, "La Grupera," ca. 10 m, 11°33′N, 87°48′W, *Moreno & Sandino 14709* (MO); E of campo Germán Pomares, ca. 60–90 m, 11°36′N, 83°52′W, *Moreno 15137B* (MO); ca. 10 m, 11°36′N, 83°51′W, *15187* (MO); Caño Monte Cristo, 1 km before the camp Germán Pomares, ca. 10 m, 12°35′N, 83°51′W, *Moreno 14839* (MO); *14843B* (MO); "Kurinwacito," 80–100 m, 13°08′N, 84°55′W, *Moreno 23699* (F, MO); Cerro El Ocote, 700 m, 13°38′43″N, 85°07′06″W, *Ortiz 1093* (MO); Comarca El Hormiguero, W of Río Uli, *Neill 1921* (MO); Mpio. Rama, Loma Buena Vista, 100–150 m, 12°08′N, 84°12′W, *Robleto 620* (MO); Mpio. Siuna, Siunawás, ca. 200 m, 13°43′N, 84°45″W, *Ortiz 1481* (MO); Santa Rosa, *Ortiz 102* (MO); Negro Wás Sector, El Empalme–Rosita, <200 m, ca. 13°45′N, 84°25′W, *Ortiz 2163* (MO); Río Kubalí, ca. 7 km W of Río Iyas, ca. 200 m, ca. 13°29′N, 85°16′W, *Stevens & Moreno 19278* (MO); Río Matís, Waní–Siuna, ca. 0–100 m, ca. 13°43′N, 84°49′W, *Pipoly 4685* (MO); ca. 0–100 m, *Stevens 4686* (MO. PANAMA. **Bocas del Toro**: S end, Cayo García, 0–5 m, *Peterson & Annable 7287* (MO); Chiriquí Lagoon, *von Wedel 1253* (GH, MO); *2668* (GH, MO); Gualaca–Chiriquí Grande, 4.2 mi. S of Chiriquí Grande, near sea level, 8°55′N, 82°09′W, *Croat 66813* (MO, TEX); Changuinola–Almirante, Station Milla 7.5, <100 m, *Croat 38130* (MO); Río Oeste, S of Almirante, 5 m, *Peterson & Annable 7226* (MO). **Canal Area**: end of Pipeline Road, 19 km NW of Gamboa, 25–50 m, *Nee & J. D. Smith 11070* (MO, US); Fort San Lorenzo, *Maxon & Valentine 7001* (US); 40 m, 9°03′N, 79°37′W, *Croat 69834* (B, CAS, CR, MO); near Madden Dam and along Azote Caballo Road, near Alahuela, 90–100 m, *Dodge 16592* (MO); road to Fort Gulic, *Lazor & Blum 5412* (MO, NY); Barro Colorado Island, *Croat 6586* (MO, NY, US); *Wetmore & Woodworth 874* (GH); *Welch 19833* (MO, NY); *Croat 6066* (MO); *11758* (MO); *9223* (MO); *5878* (MO); *10357* (MO); *12802* (MO); *10744* (MO); *Starry 24* (MO); *Netting 60* (MO); *Hutchison & Wright 2920* (NY, US); *Croat 11744* (MO, SCZ); *10383* (MO, SCZ); *7129* (MO, SCZ); Madden Forest Preserve, vic. George W. Green Park, *Welch 19853* (MO, NY, RSA); Río Pequení, near Salamanca Hydrographic Station, 70–80 m, *Dodge et al. 16592a* (MO); Curundu, 8°58′N, 79°32′55″W, *Croat & Zhu 76204* (MO). **Chiriquí**: W of Gualaca, 100 m, 8°29′N, 82°17′W, *Churchill & de Nevers 4482* (MO, RSA). **Coclé**: El Valle de Antón, *Folsom & Kauke 2776* (MO); *Kennedy et al. 2209* (MO, US). **Colón**: near Palmas Bellas, *Thoms 47* (MO); vic. of Miguel de la Borda, *Croat 9895* (MO); *9885* (MO); 10 mi. SW of Portobelo, 2–4 mi. from coast, 10–200 m, *Liesner 1103* (MO, NY, US); Portobello, 5–100 m, *Pittier 2424* (US); France Field–Catival, *Standley 30439* (US); Río Guanche, *D'Arcy 9724* (MO); *Gentry 6313* (MO); 100 m, 9°30′N, 79°39′W, *Croat 75193* (MO). **Darién**: 3 mi. N of Santa Fe, *Tyson et al. 4616* (MO, SCZ); Canglón–Yaviza–Río Chucunaque, 7.7 mi. E of Canglón, 50 m, 8°20′N, 77°50′W, *Knapp & Mallet 3944* (MO, US). **Los Santos**: Tonosí–Jobero, 50–80 m, *Croat 34454* (MO). **Panamá**: Corozal Road, near Panamá, *Standley 26861* (US); *26841* (US); Río Tapia, *28112* (US); 4 mi. E of Panama City, road to Tocumen, *Tyson 3483* (FSU, MO, SCZ); Cerro Jefe region, *D'Arcy et al. 15520* (MO); 9°15′N, 79°30′W, *Croat & Zhu 76215* (CR, MO, P, TEX); San José Island, *Johnston 718* (GH); *919* (GH); *921* (GH, US). **San Blas**: Nusagandi, El Llano–Cartí road, Mile 10.3, 300 m, 9°20′N, 79°W, *Croat & Zhu 76576* (MO). **Veraguas**: S of Santa Fe, ca. 450 m, *Nee 8041* (MO); Bahía Honda, *Elmore H30* (US); ca. 1 km above Cañasas on road to Los Valles, 230 m, *Croat 37063* (MO).

Philodendron hederaceum var. **kirkbridei** Croat, var. nov. TYPE: Costa Rica. Alajuela: eastern rim of Laguna Hule, ca. 1.5 km N of Angeles, along road through pasturelands, 840–860 m, 8 July 1972, *Luteyn 3350* (holotype, MO–2173874; isotype, DUKE). Figure 224.

Planta hemiepiphytica; internodia 2–28 cm longa, 1–2.5 cm diam.; cataphylla 6–19 cm longa, incostata aut interdum leniter 2-costata, decidua intacta; petiolus (6.5)8–22.5 cm longus, 3–6 mm diam.; lamina (11)16–29.5(42) cm longa, (8)10.3–23(35) cm lata; inflorescentia 1; pedunculus 5.5–7.5 cm longus; spatha 14–24 cm longa, lamina spathae flaviviridis, extus cremascenti vs. apicem, intus pallidius viridi; pistilla 5-locularia; loculi 20–25-ovulati; loculi cum ca. 24-seminibus.

Hemiepiphyte; internodes 2–28 cm long, 1–2.5 cm diam., weakly flattened on one side with two sharply raised ribs on the side above petiole, very weakly sulcate on the opposite rounded side, prominently ribbed throughout its circumference, the ribs smooth or prominently warty, 2–28 cm long, 1–2.5 cm diam., medium to dark green, matte, drying reddish brown; cataphylls 6–19 cm long, unribbed or sometimes weakly 2-ribbed, deciduous intact; **petioles** (6.5)8–22.5 cm long, 3–6 mm diam.; **blades** (11)16–29.5(42) cm long, (8)10.3-23(35) cm wide; upper surface medium to dark green, drying brown to greenish brown, lower surface medium green, glossy, drying brown to greenish brown; primary lateral veins 3–4 per side, departing mdirib at a 45–50° angle. INFLORESCENCES 1 per axil; peduncle 5.5–7.5 cm long; **spathe** 14–24 cm long, spathe blades yellow-green becoming cream-colored toward apex outside, lighter green inside; **spadix** stipitate to 1 cm; 13–20 cm long; ovary 5-locular, 20–25 ovules per locule. INFRUCTESCENCE with about 24 seeds per locule.

Flowering in *Philodendron hederaceum* var. *kirkbridei* occurs during the late dry season and early rainy season (probably as early as March and as late as September) based on post-anthesis and early fruiting collections. No collections have been made

at anthesis. Immature fruits have been collected in April, July, and August.

Philodendron hederaceum var. *kirkbridei* ranges from Costa Rica to Ecuador at (250)300 to 900 m in *Premontane wet forest* and *Tropical wet forest.* The variety has been collected only once in both Suriname and Ecuador. It was collected in Ecuador at Reserva ENDESA (0°5′N, 79°02′W), an area of *Premontane rain forest.* It is to be expected in Colombia.

This variety is recognized by its scandent habit, slender stems, petioles shorter than the blades, ovate-cordate brownish-drying blades and especially by its dried stems, which are reddish brown and conspicuously ribbed. Specimens from Panama have stems also conspicuously and densely warty while specimens in Costa Rica have stems reddish brown and conspicuously ribbed but are smooth rather than warty.

The variety differs from the autonymic variety primarily in occurring at generally higher elevations in wetter forests and by its reddish brown, conspicuously ribbed stems. In parts of Central America and in South America where both species occur, *P. hederaceum* var. *kirkbridei* occurs usually above 500 m in *Premontane wet* and *Tropical wet* forests. In contrast, *P. hederaceum* var. *hederaceum* has stems that dry smooth and green and occur primarily in tropical moist forest. Though there is overlap in the elevation range and even life zone (both may sometimes be found in *Premontane wet forest*), the two varieties do not occur in the same sites and can be readily distinguished by their stems.

Philodendron hederaceum var. *kirkbridei* is named in honor of Joseph Kirkbride (BARC), who first collected the taxon in 1968 on Cerro Caracoral in Coclé Province in Panama while a graduate student at the Missouri Botanical Garden.

Additional specimens examined. COSTA RICA. **Alajuela**: Cañas–Upala, 8 km N of Bijagua, 300 m, *Croat 36498* (MO); Cariblanco, 900 m, 10°15′N, 84°11′W, *Lent 3591* (F). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35837* (MO). PANAMA. **Coclé**: 710–800 m, 8°39′N, 80°36′W, *Croat 68758* (MO, PMA, US); Cerro Caracoral, *Kirkbride 1098* (MO); Alto Calvario, 9.4 km above El Copé, 750–900 m, *Croat 44741* (MO); La Mesa, above El Valle de Antón, 900–930 m, *Croat 37471* (MO); Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67236* (MO). **Colón**: Río Piedras, Río Piedras Lumber Road, 6.7 mi. E of Sabanitas, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75158* (MO, PMA). **Panamá**: El Llano–Cartí Road, 12 mi. above Pan-American Highway, 200–500 m, *Croat 22909* (MO); Mile 7, near El Llano, 460 m, 9°19′N, 79°59′W, *Croat 75108* (MO, PMA, US); Km 12–16, *Kennedy et al. 3146* (MO, US). **San Blas**: 1 mi. S of Nusagandi, 9 mi. N of Interamerican Highway, 350 m, 9°20′N, 79°W, *Croat & Zhu 77001* (CM, MO).

ECUADOR. **Pichincha**: between Quito and Puerto Quito, Km 113, 800 m, 0°5′N, 79°2′W, *Rodríguez 282* (MO).

Philodendron hederaceum var. **oxycardium** (Schott) Croat, stat. et. comb. nov. Basionym: *Philodendron oxycardium* Schott, Syn. Aroid. *Philodendron scandens* subsp. *oxycardium* (Schott) G. S. Bunting, Gentes Herb. 10: 163. 1968. TYPE: Mexico: exact origin unknown (holotype, W? lost). Schott ic. 2714 (neotype, here designated, W). [See fig. 17 in Bunting, 1968.]

Internodes smooth, sometimes with 2 ridges or weakly angular on one side, semiglossy, 5–26 cm long, to 1 cm diam., usually longer than broad, drying greenish to pale brownish green; cataphylls 19 cm long, unribbed, green; **petioles** 8–23 cm long; **blades** broadly ovate, semiglossy, long-acuminate to abruptly acuminate at apex, cordate at base, 26–32 cm long, 18–22 cm wide (ca. 1.5 times longer than wide), 2.5–3 times longer than petiole, broadest near the middle, upper surface bright green, lower surface yellow-green; sinus narrowly triangular to closed, to 5 cm deep; basal veins 2–3 per side, with 1–2 free to base, and with the first and or second free to base, 2–3 coalesced to 1 cm; primary lateral veins 2–3 per side, departing midrib at a 45° angle. INFLORESCENCES (based on dried specimen) with peduncle 4 cm long, 7 mm diam.; **spathe** 14 cm long; spathe blade 6.5 cm long; spathe tube 7.5 cm long; **spadix** sessile, cylindrical, 12 cm long; pistillate portion 4 cm long; staminate portion 8 cm long; fertile staminate portion drying reddish brown.

Flowering in *Philodendron hederaceum* var. *oxycardium* is poorly known. A single fertile collection with immature fruits in January was seen.

Philodendron hederaceum var. *oxycardium* is apparently endemic to Mexico, known only from the Gulf slope in the states of Jalisco, Nayarit, Oaxaca, San Luis Potosí, and Veracruz at 120 to 580 m, principally in areas of *Tropical moist forest.* Material of *P. hederaceum* [as *P. scandens*] collected in Jamaica (Bunting, 1968) is sterile.

Philodendron hederaceum var. *oxycardium* is similar in appearance to variety *hederaceum,* except that leaves of the former are firmer in texture and glossy in both the juvenile and adult forms. In outline, the leaf blades of *P. hederaceum* var. *oxycardium* are often somewhat broader and more abruptly acuminate than for variety *hederaceum* (Bunting, 1968). The epidermal cells have a more or less

flattened epidermis on the upper surface (Bunting, 1968), which causes it to be glossy. In contrast, the epidermal cells of *P. hederaceum* var. *hederaceum* are mounded and sometimes conical, giving leaves of that variety their characteristic velvety sheen.

Though Bunting (1968) treated this taxon as a subspecies, it appears to overlap geographically with the typical material so it will be treated here as a variety.

Additional specimens examined. MEXICO. **Nayarit**: San Blas, *Ferris 5440* (DS). **Oaxaca**: Tuxtepec–Oaxaca, 6–14 mi. from bridge at Valle Nacional, ca. 580 m, *Moore & Bunting 8905* (BH). **San Luis Potosí**: N of Tamazunchale, *Clark 7408* (MO, NY); Tamazunchale, 120 m, *Aguirre & Reko 334* (NY). **Veracruz**: 5.7–6 mi. from Catemaco on road to Sontecomapan, ca. 380 m, *Moore & Bunting 8937* (BH); just before Papantla on road from Tecolutla, *Moore & Bunting 8953* (BH); NW of Misantla, 2.4 mi. on road to Martínez de la Torre, ca. 320 m, *Moore & Bunting 8944* (BH); Conejo–Huatusco, Km 45, near Puente Nacional, slopes of barranca de Santa María across highway from Hacienda El Mirador, *Moore & Bunting 8869* (BH); Dist. Papantla, *Kelly 16* (BH).

Philodendron heleniae Croat, sp. nov. TYPE: Panama. San Blas: El Llano–Cartí road, 14 km N of Pan-American Hwy., 300 m, 9°15′N, 79°W, 12 July 1988, *Croat 69244* (holotype, MO–3599872; isotypes, B, CAS, COL, CR, F, K, MEXU, NY, PMA, SCZ, US, VEN). Figures 227–230.

Planta plerumque hemiepiphytica, raro terrestris; internodia 4–12 cm longa, 2–3 cm diam.; cataphylla 15–36 cm longa, 1–2-costata, decidua; petiolus teres aut D-formatus, 14–41.5 cm longus, 6–10 mm diam.; lamina anguste ovata, 25–52 cm longa, 6–26 cm lata, in sicco flavibrunnea; inflorescentia 2–10; pedunculus 2–6 cm longus, 4–6 mm diam.; spatha 5–10 cm longa, rubrimarronina; lamina spathae extus pallidiori vs. apicem, intus alba, dilute suffusa marronina; tubo spathae intus atrimarronino; pistilla (5)6–9-locularia; loculi (1)3–4-ovulati.

Usually hemiepiphytic, rarely terrestrial; vining or appressed-climbing, stem appressed-climbing to somewhat scandent, sap tannish; internodes scurfy, 4–12 cm long, 2–3 cm diam., much longer than broad, medium green, drying reddish brown, epidermis smooth or irregularly folded and ridged, sometimes fissured with minute cracks perpendicular to axis, drying with folds longitudinally and usually with fissures transversely; roots dark brown, to 50 cm long, 1–2 mm diam.; cataphylls thin, 15–36 cm long, 1-ribbed to sharply 1-ribbed, or sharply 2-ribbed, green, tinged red, speckled violet-purple, deciduous, rounded, apiculate at apex; **petioles** 14–41.5 cm long, 6–10 mm diam., ± terete or to slightly thicker than broad, or bluntly D-shaped, firm, medium green, tinged violet-purple at base and apex, bluntly flattened adaxially; geniculum 9 mm long, thicker and paler than petiole; **blades** narrowly ovate, subcoriaceous to coriaceous, strongly bicolorous, acuminate at apex (the acumen sometimes apiculate, inrolled, 5 mm long), usually weakly subcordate, sometimes obtuse, truncate or rounded at base, 25–52 cm long, 6–26 cm wide (2–3.37(4.2) times longer than wide), (1.1–1.8(2.30) times longer than petiole), upper surface dark green, semiglossy, drying yellow-brown, lower surface much paler and with dark secretory canals, weakly glossy to matte, drying yellowish to reddish brown; sinus arcuate, 1–1.5 cm deep when present; midrib broadly convex or weakly raised to flat, pale green above, bluntly acute and thicker than broad, reddish slightly paler than surface below; basal veins lacking; primary lateral veins (6–7)8–10(11–13) per side, departing midrib at a 30–40° angle, weakly and narrowly sunken above, raised and paler than surface below; minor veins weakly visible, arising from the midrib only, often interspersed with intermittent secretory ducts, the surface often minutely granular below. INFLORESCENCES 2–10 per axil; peduncle 2–6 cm long, 4–6 mm diam., green, tinged red to reddish; **spathe** recurved (curved downward), semiglossy, 5–10 cm long (1.2–2.5 times longer than peduncle), reddish maroon throughout; spathe blade paler toward apex outside, white, weakly tinged maroon inside; spathe tube 3–4 cm long, dark maroon inside; **spadix** sessile; cylindrical to clavate, protruding forward at anthesis, 5.8–7.5 cm long, ± uniform throughout; pistillate portion pale green to yellowish green, cylindrical to slightly ovoid, 2–3.5 cm long, 5–7 mm diam. throughout; staminate portion cream to white, cylindrical or clavate, 3.4–5 cm long, 6–9 mm diam. at base, 9–10 mm diam. at middle, 5–9 mm diam. ca. 1 cm from apex, broadest at or above the middle, or equally broad throughout, as broad as or slightly broader than the pistillate portion; sterile staminate portion not detectable; pistils 1.4–1.7 mm long, 0.5–1.4 mm diam.; ovary (5)6–9-locular, 0.7 mm long, 0.7 mm diam., locules 0.9–1.2 mm long, 0.3–0.4 mm diam., ovule sac 0.4–1 mm long, with sub-basal placentation; ovules (1)3–4 per locule, 1-seriate, contained within translucent ovule sac, 0.2–0.4 mm long, longer than funicle; funicle 0.1–0.2 mm long (can be pulled free to base), style 0.2–0.4 mm long, 0.4–0.6 mm diam., similar to style type B; stylar canals tiny, difficult to see emerging; style apex flat; stigma discoid or subdiscoid, unlobed, 0.4–0.5 mm diam., 0.1–0.2 mm high, covering entire style apex except for the center; the androecium truncate, margins 4–6-sided, sometimes weakly scalloped; thecae oblong, 0.1–

0.3 mm wide, ± parallel to one another. INFRUCTESCENCE with berries white, 3.3 mm long, 2.4 mm diam.; seeds ca. 6 per berry, reddish brown, 1–1.1 mm long, 0.3–0.5 mm diam.

Flowering in *Philodendron heleniae* occurs in Panama during the late dry season and much of the rainy season, March through October (except April, May, and September). South American collections broaden that range to include the whole year (January through December, except May and September). Post-anthesis collections have been made from June to October.

Philodendron heleniae ranges from Panama (to be expected in the Cordillera de Talamanca in eastern Costa Rica) to Ecuador, from 20 to about 1040(–1450) m elevation in *Tropical wet forest* and *Premontane rain forest* in Panama, Colombia, and Ecuador. In addition, it occurs in pluvial wet forest in Colombia.

Philodendron heleniae is a member of *P.* sect. *Calostigma* subsect. *Oligocarpidium*. This species is characterized by its scandent habit; internodes much longer than broad drying with longitudinal folds and usually transverse fissures; petioles terete to bluntly D-shaped; and narrowly ovate, subcordate, yellow-brown-drying blades with dark secretory canals visible on the lower surface. Especially characteristic are the clusters of 2–10 small inflorescences with externally red spathes.

Philodendron heleniae can be confused with *P. lentii*, which also comprises more or less scandent plants with subcordate leaf blades. That species differs, however, in having one to two large, mostly white inflorescences per axil and more broadly ovate blades drying with many, pale, sunken veins on the upper surface and no dark secretory vessels on the lower surface.

Specimens from the Pacific slope of South America (e.g., *Croat 58424, Tipaz et al. 1318*) are on average larger, with leaves ranging up to 60 cm long and 30 cm wide and with spathes occasionally to 12 cm long. Still, these probably do not differ sufficiently to represent even another subspecies.

Lawrance 817 from Boyacá Department at El Humbo (at 914 m in the Río Magdalena drainage) in Colombia closely matches the material from the Pacific slope. If it proves to be *P. heleniae* it would be the first collection from the Eastern Cordillera of the Andes.

Some South American collections from the Amazon basin may belong to this species. These collections are from both Colombia (*Pipoly et al. 15892, 16027* in Amazonas) and Ecuador (*Gudiño 1160* and *Thomas & Ríos 6708* in Pastaza Province and *Cerón 3360* and *Bennett et al. 4526* in Napo Province). However, most of the collections from the Amazon basin do not mention spathe color, although *Gudiño 1160* indicates the spathes to be greenish red.

Particularly interesting is *Thomas & Ríos 6708*, with spathes described as becoming creamy white, something that never happens with Central American material of *Philodendron heleniae*.

The species was first collected in 1970 by Jim Luteyn and Helen Kennedy in the vicinity of El Valle in Coclé Province, Panama. It is named in honor of one of the collectors, Helen Kennedy, who at the time worked for the Missouri Botanical Garden as the Curator of Summit Herbarium.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, 6.6 mi. N of bridge over Fortuna Lake, 780 m, 8°45′N, 82°18′W, *Croat 66780* (MO). **Coclé**: El Valle region, La Mesa, 800–900 m, 8°38′N, 80°09′W, *Croat 67154* (AAU, CM, KYO, L, MEXU, MO, PMA, TEX, US); El Valle, 5 mi. N of town, 2200 ft., *Hammel & Kress 13427* (DUKE); 8 mi. N of El Valle ca. 880 m, *Luteyn & Kennedy 1734* (DUKE); 880 m, *Croat 37576* (MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76738* (AAU, CM, DUKE, M, MO, S, SEL, TEX); slopes of Cerro Gaital, 800–900 m, 8°37′N, 80°07′W, *McPherson 11209* (L, MO, NY, P). **Darién**: Río Tuquesa, 2 km by air from Continental Divide, vic. of mining camp of Tyler Kittredge, *Croat 27097* (CAS, F, K, MO, PMA, US). **Panamá**: El Llano–Cartí Road, 10.1 mi. above Inter-American Highway, 325–350 m, *Croat 67351* (MO, NY, PMA, US, WIS); Mile 6.8, 350 m, *49106* (MO); Mile 10, 330 m, *33778* (F, MO), *33817* (MO); Mile 7, 460 m, 9°19′N, 79°59′W, *75114* (CAS, MO); 550 m, 9°43′N, 78°60′W, *60502* (MO); Mile 10.6, ca. 400 m, 9°17′N, 78°58′W, *Miller et al. 869* (HUA, MO, PMA); El Valle de Madroño–La Saena, 2.5 mi. N of El Valle de Madroño, 180 m, 9°14′25″N, 79°05′W, *Croat & Zhu 77048A* (MO); Cerro Jefe–Cerro Brewster ["Panama/San Blas"], 600–800 m, 9°17′N, 79°17′W, *Hammel & de Nevers 13553* (MO). **San Blas**: El Llano–Cartí Road, 1–5 mi. N of Nusagandi, 250–300 m, 9°16′N, 79°W, *Thompson 4660* (CM, MO); Nusagandi–Cartí Road, 400 m, 9°18′N, 78°58′W, *McDonagh et al. 93* (BM, MO); ca. 350 m, ca. 9°15′N, 79°W, *McPherson 9762* (MO); 350 m, 78°15′W, 9°19′N, *de Nevers & Todzia 3530* (COL, MO, PMA, QCA, RSA, TEX); 10.1 mi. N of Interamerican Highway, then ca. 0.5 mi. N, Paseo Mariska near road, 300 m, 9°20′N, 79°W, *Croat & Zhu 77020* (MO); El Llano-Cartí Road, 23–29 km from Pan-American Highway, 300–400 m, 9°22′N, 78°69′W, *Knapp 1830* (MO); *1840* (MO, PMA); Km 15, 350 m, 9°20′N, 78°58′W, *Galdames et al. 1288* (PMA); km 17–19, 350 m, 9°19′N, 78°55′W, *de Nevers & Herrera 7963* (CM, MO, US); Cerro Obu, 400–500 m, *de Nevers et al. 8068* (MO, NY). **Veraguas**: Santa Fe region, Alto Piedra–Calovébora, Río Dos Bocas Valley, 350–400 m, *Croat 27370* (F, K, MO, PMA); *27397* (MO).

COLOMBIA. **Antioquia**: Medellín–Bogotá, 12.4 km from entrance to San Luis 800 m, 5°59′N, 74°59′74″W, *Betancur et al. 622* (MO); 4.8 km E of San Rafael, 1040 m, 6°18′N, 75°W, *Brant & Roldán 1486* (HUA); Quebrada Honda, Río Guatapé, *Orozco et al. 898* (COL); Río Guatapé, 1250 m, *Orozco et al. 955* (COL); San Carlos, Finca

"El Desespero," Alto de Samaná, near Miraflores, 4 hrs. SW of Alto de Samaná, 710–820 m, 6°5′N, 74°56′W, *Callejas et al. 8628* (NY); San Luis, Medellín–Bogotá, La Tebaida, 1010–1060 m, 6°8′N, 75°10′W, *Callejas et al. 4015* (MO); Sector Río Samaná–Río Claro, 750 m, *Hernández et al. 551A* (HUA); San Luis–Puerto Triunfo, SE of Granada, S of San Carlos, ca. 3 km SE of San Luis, ca. 800 m, 5°57′N, 74°57′W, *Croat 52038* (COL, MO, NY); Gómez Plata–Yolombo border, Sector La Cancana, along Río Porce, km 14 via Amalfi, 1030 m, *Callejas et al. 2338* (MO); Sonson, Rioverde region, Hacienda "La Soledad," on the banks of Quebrada "Curubital," *Gutiérrez 35552* (UC); Amalfi–Fraguas, NE of Salazar, 23–26.5 km from center of Amalfi, 1220–1300 m, 6°58′N, 74°59′W, *MacDougal et al. 4042* (MO). **Chocó**: Bahía Solano, S of airport, ca. 100 m, 5°13′30″N, 76°21′30″W, *Croat 57458* (CHOCO, COL, JAUM, MO, US); ca. 2 km E of Playa de Oro, ca. 200 m, 5°20′N, 76°23′W, *Croat 57424* (CHOCO, COL, MO); Mecana (N of Bahía Solano), Quebrada Resaquita, 30 m, *Juncosa 2536* (MO); Quibdó–Istmina, 6.6 km S of Quibdó, <100 m, 5°33′N, 76°37′W, *Croat & Cogollo 52156* (MO); Río Pató, Las Animas–Pató, Serranía de Baudó, 10 km SE of Pató, 5°17′N, 76°45′W, *Croat 56071* (MO), *Croat 56107* (MO); Río Sucio, Cerro del Cuchillo, zona de Urabá, 520 m, *Cárdenas 468* (MO); Parque Nacional de Utría, Río San Pichí, 0–100 m, 6°20′N, 77°20′W, *García & Agualimpia 458* (MO); Río San Juan, Quebrada del Taparal, 5–20 m, *Cuatrecasas 21462* (F). **Risaralda**: Mpio. Mistrato, corregimiento San Antonio de Chamí, vereda la Unión, carretera hacia La Mesenia, 1450–1700 m, 5°28′N, 75°54′W, *Betancur et al. 3520* (MO). **Valle**: Cali–Buenaventura, Río Digua valley, 1 km E of La Cascada, 340 m, *Croat 38579* (MO, PMA); Bajo Calima area, Quebrada La Sierpe, 5 m, 4°10′N, 77°10′W, *Forero et al. 4006* (MO); Bahía Málaga, 0–20 m, 4°N, 77°30′W, *Gentry et al. 53362* (MO); carretera Gasolina 6 km S of main road between Calí–Buenaventura highway and Málaga, 50–80 m, 3°56′N, 77°07′30″W, *Croat 69411* (CM, MO); 22.3 km beyond Pulpapel Headquarters, 4°02′N, 77°07′W, *Croat 61275* (CUVC, MO). ECUADOR. **Carchi**: Tulcán, Reserva Indígena Awá, 650–100 m, 1°N, 78°24′W, *Tipaz et al. 1318* (MO, QCNE). **Esmeraldas**: Lita, 550–650 m, *Madison et al. 4990* (F, K, SEL); Lita–San Lorenzo, Km 18, 0°55N, 78°28W, *Croat 72389* (MO); San Lorenzo, Mun. Ricaurte, Reserva Indígena Awá, 300 m, 1°10′N, 78°32″W, *Tipaz et al. 2068* (MO); Río Jordán, NE of Las Golondrinas, near San Isidro, 300 m, 0°20′N, 79°12′W, *Palacios 11485* (MO, QCNE). **Imbabura**: Lita, 600 m, *Cobb 29* (MO). **Pichincha**: Río Verde, 2 km SE of Santo Domingo de Los Colorados in Cooperative Santa Marta #2, 530 m, *Dodson 7403* (MO, QCNE); Santo Domingo de los Colorados, Río Baba, 28 km S, 350 m, *Dodson & Thien 1187* (MO).

Philodendron immixtum Croat, sp. nov. TYPE: Panama. Panamá: Comarca de San Blas, Río Playón Chico, 50–100 m, *H. Herrera et al. 1167* (holotype, MO–4256423; isotypes, AAU, K, MEXU, PMA, US). Figures 233–236.

Planta hemiephytica; internodia (2)10–15 cm longa, (7 mm) 1–1.5 cm diam.; petiolus subteres, actue D-formatus ad debiliter planatus; lamina anguste ovata vel ovato–elliptica. 16–36 cm longa, 5–12 cm lata; inflorescentia solitaria; pedunculus 5–13 cm longus; spatha 9–19 cm longa, lamina albo-viridis vel alba, tubo viridis extus, rubo vel purpureo intus; spadix 10–11 cm longus; ovarium (3)4–6(8)-loculare; loculi 1(2) ovulati.

Hemiepiphytic; stem scandent, sap reddish, watery; internodes long, slender, ± glaucous, (2)10–15 cm long, (0.7)1–1.5 cm diam., much longer than broad, dark olive-green matte to weakly glossy, becoming gray-green, drying light brown, epidermis sometimes cracking with loose flakes; roots ca. 5 per node, to 15 cm long, 2–3 mm diam., tannish gray, drying reddish brown, ± smooth, long; cataphylls somewhat spongy, to 17 cm long, unribbed, weakly 2-ribbed or sharply (1–)2-ribbed (ribs 2 mm high), pale green, dark short-lineate, drying pale brown to yellowish brown, usually some deciduous, sometimes persisting somewhat intact, eventually fibrous, obtuse at apex, margins paler, yellowish; **petioles** 7.5–16(21) cm long, 2–10 mm diam., subterete, sharply D-shaped to slightly flattened adaxially, rounded abaxially, surface dark green-striate, matte to semiglossy, shortly dark lineate, with dark green ring around apex; **blades** narrowly ovate to ovate-elliptic, or rarely oblong-elliptic, subcoriaceous, semiglossy, strongly bicolorous, abruptly acuminate at apex (the acumen tightly inrolled to apiculate, 2–4 mm long), subcordate, rarely rounded at base, 16–36 cm long, 5–12 cm wide (1.9–3.7 times longer than wide), (1.3–3.1(3.8) times longer than petiole), about twice as long as petiole, broadest below middle, margins narrowly hyaline, upper surface drying green to grayish to brownish green; posterior lobes short, about as broad as long and held close to petiole; sinus shallow, 0–2.5(3) cm deep; midrib flat to weakly convex, concolorous or slightly paler than surface above, convex to bluntly acute, paler than surface below; basal veins lacking; primary lateral veins 4–8 per side, departing midrib at a 50–60° angle, ± straight to weakly arcuate to the margins, sunken and paler than surface above, weakly raised and darker than surface below; interprimary veins weakly raised and darker than surface; minor veins distinct to weakly visible, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 5–13 cm long, 3–7(11) mm diam., dark green; **spathe** 9–19 cm long, (1.1–2.1 times longer than peduncle), green, densely and obscurely short-lineate, narrowly acuminate at apex; spathe blade pale greenish white to white outside, pale greenish white, dark lineate inside; resin canals appearing as continuous lines, drying reddish brown, resin droplets forming on spathe surface within; spathe tube dark green in back, paler in front on open edges outside, red or violet-purple inside; **spadix** gradually tapered to apex,

protruding out of the end of spathe, bluntly rounded to obtuse at apex, 10–11 cm long, broadest above the middle, constricted slightly above sterile staminate portion; pistillate portion pale green, cylindrical, 3.4–4.2 cm long, 3.7 cm long in front, 2.7 cm long in back, 9–11 mm diam. at apex, 10–11 mm diam. at middle, 9–11 mm wide at base; staminate portion 6.8–7.5 cm long; fertile staminate portion white, cylindrical to clavate, 9–12 mm diam. at base, 1.1–1.3 cm diam. at middle, 7–12 mm diam. ca. 1 cm from apex, broadest at the middle, broader than the pistillate portion, broader than the sterile portion; sterile staminate portion as broad as, narrower than, or broader than the pistillate portion, ± 12 mm diam.; pistils 1.9–2.3 mm long, 1.3–1.9 mm diam.; ovary (3)4–6(8)-locular, walls sometimes embedded with granular, crystal-like particles, locules 0.7–1.3 mm long, 0.4–0.7 mm diam., ovule sac 0.6–1.3 mm long, with subbasal placentation; ovules 1(2) per locule, contained within transparent ovule sac, 0.4–0.7 mm long, longer than funicle; funicle 0.2–0.6 mm long (can be pulled free to base), style 0.3 mm long, 0.9–1.4 mm diam., similar to style type B; stigma subdiscoid, unlobed, 0.7–0.9 mm diam., 0.2 mm high; the androecium truncate, margins 4–6-sided; thecae oblong to slightly elliptical, 0.4 mm wide, ± parallel to one another; sterile staminate flowers 4–6-sided, 1–1.8 mm long, 1.1–1.7 mm wide. INFRUCTESCENCE with spadix yellowish orange, 8 cm long, 3 cm wide; berries concave at apex; seeds 1 per locule, 1.5–1.8 mm long, 0.6–0.7 mm diam., yellow-brown.

Flowering in *Philodendron immixtum* occurs during the last half of the dry season and the first part of the rainy season, March through May, with post-anthesis inflorescences seen from March through August, and fruits seen in July.

Philodendron immixtum ranges from Panama to Colombia (Golfo de Urabá), occurring at or near sea level (to ca. 140 m elevation), primarily along the Atlantic slope in Colón and Panamá Provinces but also in Panamá Province on the Pacific slope along the Río Majé. It occurs in *Tropical wet forest, Premontane wet forest,* and in wetter parts of *Tropical moist forest* life zones.

Philodendron immixtum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* The species is characterized by its scandent habit; long, slender, mostly light-brown-drying internodes; slightly flattened petioles (about one-half or less as long as the blade); narrowly ovate to ovate-elliptic, green-drying blades, which are usually cordulate at the base; as well as by the solitary inflorescence with a green spathe, the base white on the blade at anthesis and red within on the tube.

The species has been confused with *P. inconcinnum* Schott (1856) (hence the name "immixtum," meaning "intermixed or mingled with") from Venezuela (Standley, 1944; Croat, 1978). The Schott paintings of *P. inconcinnum* show a single unattached leaf and unattached inflorescences and probably represent the same species as *P. sphalerum* Schott (1860). Schott paintings of *P. sphalerum* show some leaves that are virtually identical to the above-mentioned drawings. *Philodendron sphalerum* differs from *P. immixtum* in having several small inflorescences per axil (rather than one, somewhat larger inflorescence for *P. inconcinnum*). Schott's original description of *P. sphalerum* did not mention an inflorescence, so his drawing of that must have come later than his description. Schott's original description of *P. inconcinnum* cited Venezuela as the type locality, not Panama, and the solid greenish inner spathe surface depicted in his paintings corresponds well to *P. sphalerum* but not to the material in Panama, which has a reddish interior spathe surface.

Philodendron immixtum has also been confused with *P. ligulatum.* The latter species differs in having blades that are typically more nearly oblong-elliptic to narrowly obovate-elliptic, frequently broadest above the middle, and drying usually much blackened. In addition, it has petioles that bear a conspicuous purple ring around the petiole at the apex. In contrast, the blades of *P. immixtum* typically dry grayish to brownish green and are broadest frequently below the middle. The species also differs in having petioles that lack the purple ring at the apex.

A number of sterile or immature collections from Nicaragua may represent this species, but if so it is curious that the species has not been collected in Costa Rica (or for that matter, not further west in Panama than Miguel de La Borda in Colón Province).

Additional specimens examined. PANAMA. **Canal Area**: Balboa, *Standley 28542* (US); Ft. Randolph, *28616* (US); road between Gatún Locks and Ft. Sherman, ca. 1 mi. E of Ft. Sherman, <25 m, 9°19′N, 79°57′30″W, *Croat & Zhu 76282* (CR, GB, MO, PMA, TEX, US); Ft. Sherman, from Pina to 3 mi. NE, *Liesner 1382* (MO, US); Barro Colorado Island, *Croat 5064* (MO), *10865* (MO, SCZ); *Shattuck 851* (F, MO); *Wetmore & Woodworth 11* (F, GH); *Aviles 89* (F); *Fairchild 3079* (US); Parque Nacional Soberania, 140 m, 9°06′20″N, 79°37′20″W, *Croat & Zhu 76987* (MO). **Colón**: 0.25 mi. N of María Chiquita on road to Portobelo, *11360* (F, MO); Río Indio–Miguel de la Borda, along ocean trail, 0 m, *36898* (MO); vic. of San Miguel de la Borda, *9896* (MICH, MO, NY, PMA, SCZ); 2 mi. W of Portobelo, *33574* (BR, DUKE, MO); Palma Bellas–Sal-

ud, near sea level, *36865* (MO); 4.5 km SW of Piña, 0–5 m, *Nee 11713* (MO); 3 km S of Piña, 50 m, *Sullivan 137* (MO); Portobelo, *Croat & Porter 15613* (MO); Nuevo Tonosí–Río Indio, near sea level, *Croat 33545* (MO). **Darién**: Cerro Pirre, 17 km N of El Real, along Río Perisenico, 100 m, 8°01′N, 77°44′W, *Croat & Zhu 77093* (CM, MO); *77162* (CM, MEXU, MO, PMA, US). **Panamá**: Río Maje, W of Bayano Lake, ca. 2 mi. upstream, 30–60 m, *Croat 34592* (MO).

COLOMBIA. **Chocó**. Mpio. Acandí, Golfo de Urabá, Bahía Zardí, 0–5 m, 8°23′N, 77°07′W, *Betancur et al. 1238* (HUA, MO).

Philodendron jacquinii Schott, Syn. Aroid. 90. 1856. TYPE: Plate 152 in Jacq., Select Stirp. Amer. Hist. 1763 (holotype). Figures 231–232, 237, 241–242.

Philodendron hoffmannii Schott, Oesterr. Bot. Z. 8: 178. 1858 (as "*P. hoffmanii*"). TYPE: Costa Rica. *Hoffmann s.n.* (holotype, B destroyed). Schott ic. 2507 (neotype, here designated, W).

Philodendron deviatum Schott, Bonplandia 7: 29. 1859. TYPE: Venezuela, *Fendler 1329* (lectotype, here designated, K).

Philodendron erlansonii I. M. Johnston, Sargentia 8: 89, t. 13. 1949. TYPE: Panama. Panamá: Perlas Archipelago, San José Island, along road about one-half mi. E of Red Hill, 31 Dec. 1945, *Johnston 967* (holotype, GH).

Philodendron apocarpum Matuda, Madroño 10: 171. 1950. TYPE: Mexico. Chiapas: along Río Cintalapa, at Gilguero, 15 km E of Escuintla, Chiapas, ca. 200 m, 10 Aug. 1948, *Matuda 18313* (holotype, MEXU; isotypes, F, MEXU).

Hemiepiphytic vine; stem scandent, green to gray-brown, glossy, setose-pubescent; leaf scars conspicuous, 1 cm long, 1 cm wide; internodes elongate, 6–25 cm long, 0.8–1.5 cm diam., longer than broad, brownish gray, semiglossy, weakly asperous, epidermis paper-thin, sometimes peeling with age, drying gray-green to yellowish green, matte, sometimes almost blackened, larger stems drying yellow-brown and finely ridged; roots few per node, short, ca. 1 mm diam., light brown, sparsely scaly; cataphylls unribbed, semiglossy, 6–10 cm long, light green, translucent, drying cream-colored, deciduous intact; **petioles** 7.5–44.5 cm long, 5–10 mm diam., subterete, medium green, weakly glossy, narrowly and obtusely sulcate adaxially, surface setose-pubescent, often puberulous; **blades** broadly ovate-cordate, thin, chartaceous, acute to shortly acuminate, sometimes mucronate at apex (the acumen sometimes apiculate, 1–3 mm long), cordate at base, (10.5)11.5–39 cm long, 7.5–28 cm wide (0.99–1.8 times longer than wide), (0.6–1.85 times longer than petiole), usually about equal in length to petiole, broadest near point of petiole attachment, upper surface dark green, matte to subvelvety to weakly glossy, lower surface moderately paler, weakly glossy to almost matte, moderately paler; anterior lobe 8.3–27 cm long, 9–28 cm wide (1.6–3.4 times longer than posterior lobes); posterior lobes ± rounded, 3–13.5 cm long, 3.4–13.6 cm wide, directed inward at maturity, rounded or obtuse; sinus ± narrowly parabolic; midrib broadly convex, concolorous above, broadly convex to round-raised, often setose-pubescent near base, slightly paler below; basal veins 3–6 per side, with 0–1 free to base, 1–2 coalesced 0.5–2.5 cm; posterior rib not naked or briefly naked for 0.5 cm (rarely to 1.5 cm); primary lateral veins 2–3(4–5) per side, departing midrib at a 45–55° angle, ± straight to the margins, prominently impressed to weakly convex above, convex to round-raised below; minor veins arising from both the midrib and primary lateral veins; tertiary veins obscurely visible to raised and conspicuous, darker than surface below. INFLORESCENCES erect, 1 per axil; peduncle (2)4–15 cm long, (2)3–6(7–13) mm diam., green, dark-striate, glabrous; **spathe** 10–16.5 cm long, (0.96–2.3(2.7–3) times longer than peduncle); spathe blade green outside, red inside; spathe tube inflated bulbous, green outside, 4 cm long, white or green inside; **spadix** sessile; 8–13 cm long, narrowly rounded at apex; pistillate portion 3–3.5 cm long, 3.5 cm long in front, 3 cm long in back, 3.5 cm diam. throughout; staminate portion 9.2 cm long; fertile staminate portion 1.5–1.6 cm diam. at base, 1.1 cm diam. at middle, 1 cm diam. ca. 1 cm from apex; sterile staminate portion narrower than the pistillate portion, 1.2–1.5 cm diam.; pistils 6.5–7.2 mm long, 2 mm diam.; ovary 4-locular, locules ca. 1.3 mm long, ca. 0.6 mm diam., with sub-basal placentation; ovules 2 per locule, contained within transparent, gelatinous matrix (no true envelope), 0.6–1 mm long, as long as or longer than funicle; funicle 0.4 mm long (can be pulled free to base), style similar to style type B; style apex quite rounded; styles usually elongated to 5 mm long, sometimes essentially sessile; stigma hemispheroid to sometimes somewhat globular, lobed, 3.3 mm diam., 1.5 mm high, covering entire style apex; the androecium truncate, prismatic, some oblong, margins irregularly 4–6-sided, 1–1.7 mm long; thecae oblong, 0.5 mm wide, ± contiguous; sterile staminate flowers irregularly 4–5-sided, 2.2 mm wide. INFRUCTESCENCE usually pendent, often from leafless stems; peduncle 7–15 cm long, recurved; spathe falling free; spadix (2.5)5–9(14) cm long, (1.5)2.5–7 cm wide; berries greenish when immature, pale orange to red to reddish orange when mature, irregular, 1 cm long, 5 mm diam.; seeds 4–6 per berry, white, ovoid, 4 mm long, 3–4 mm diam., moderately sticky. JUVENILE

plants with petiole margins vaginate-winged almost to one-half their length; blades narrowly ovate-cordate.

Flowering in *Philodendron jacquinii* occurs in August but most post-anthesis collections are from the rainy season, mostly June through September (but also November, January, and March). Immature fruits are known from virtually throughout the year, and mature fruits from March, June, and July. There seems to be little phenological variation in this species.

Philodendron jacquinii ranges from Mexico to Panama on both slopes of the Continental Divide to northern Colombia, Venezuela, and the Guianas, as well as western Cuba and the Cayman Islands, from sea level to 1500(2500)m elevation (mostly below 300 m), mostly in *Tropical moist forest* but also in *Tropical dry forest, Premontane moist forest,* and *Premontane wet forest* life zones.

This species, the only member of *P.* sect. *Macrogynium,* is distinguished by occurring in moderately low, dry habitats, and by its scandent habit, elongate internodes, setose-pubescent stems, petioles and veins of lower blade surfaces, subterete petioles (about equal the blades in length), and thin, ovate-cordate veiny blades. Especially characteristic are the generally swollen spathe tubes and elongated styles, making the pistillate portion of the spadix much broader than the staminate portion.

Philodendron jacquinii may be confused with *P. brevispathum,* another species with scaly petioles and thin blades with prominent posterior lobes. The latter species differs in having ovate-triangular blades with more slender, frequently flaring posterior lobes and a reddish brown stem with simple or branched scales lacking the elongated setae typical of *P. jacquinii,* which has typically greenish stems. In addition, the berries of *P. jacquinii* are pale orange to reddish, and the spathe is reddish within (vs. berries whitish and the spathe green within for *P. brevispathum*).

For a discussion of the long-standing nomenclatural confusion involving *P. hederaceum,* see under the latter name. Although Standley and Steyermark (1958b), in their treatment of Araceae for the *Flora of Guatemala,* had the taxonomy correct in regards to this confusion, their illustration labeled *P. hederaceum* (fig. 58) appears to be a mixture of the two species, with the leaves of *P. hederaceum* and an inflorescence of *P. jacquinii.* The former species differs in lacking the setose-pubescence and scales characteristic of *P. jacquinii,* and in having more coriaceous blades as well as normal, short, closely compacted pistils. The spathe tube of the latter is also not markedly inflated.

A collection from El Salvador (*Croat 42075*) is unusual in lacking the usual trichomes on the stems.

Philodendron lundellii Bartlett ex Lundell (Bartlett, 1937) also corresponds to this species, but the name was invalidly published (without a description or Latin diagnosis).

Additional specimens examined. BELIZE. **Belize**: Western Highway, Mile 35, *Croat 24784* (F, MO); Belmopan, *Gentry 8423* (MO); 9.5 mi. S of Georgeville, road to Augustine, *Croat 23479* (MO); Hummingbird Highway, 7 mi. S of junction with Western Highway, N boundary of Roaring River Est., ca. 110 m, *Spellman & Newey 1967* (GH, MO). **Corozal**: *Gentle 530* (CM, MICH); Cerro Maya Ruins, Lowry's Bight, *Crane 510* (LL), *418* (LL, MO); *Gentle 345* (MICH). **Orange Walk**: Honey Camp, *Lundell 99* (F, US); 2 mi. N of Orange Walk, *Sutton et al. 122* (BM). **Toledo**: Maya Mountains, lower slopes of Richardson Peak, N of junction of Richardson Creek and Bladen Branch, 300–620 m, 88°46′30″W, 16°33–35′N, *Davidse & Brant 31955* (B, MO). COSTA RICA. **Alajuela**. Orotina, Valle del Tárcoles, 100 m, *Hammel & Grayum 19932* (CR, INB). **Guanacaste**: El Mirador, 450 m, *Aguilar et al. 1343* (INB, MO). **Heredia**: La Selva Field Station, ca. 100 m, *Hammel 10500* (MO); 1.4 km NW of Puerto Viejo, 75 m, *Anderson & Mori 25* (CM). **Puntarenas**: Barranca Site, 15 mi. N of Puntarenas, *Janzen 10742* (MO); Los Barrancas, along Pan-American Highway, near Miramar turnoff, *Gentry 774* (MO); Río Guacimal, San Luis, Monteverde, 700 m, 10°16′N, 84°49′W, *Bello et al. 20* (CR, MO); Monteverde Reserve, 1500 m, ca. 10°17′N, 84°48′W, *Croat 61192* (CM, MO); 1300 m, *Haber & Bello 7983* (CR, MO); Cantón de Buenos Aires, along Río Ceibo, Ujarrás, 500 m, 9°14′N, 83°18′W, *Grayum 10228* (CR, INB, MO, US). **San José**: Mora, Colón–Hacienda El Rodeo, 800 m, 9°55′N, 84°16′W, *Hammel 18579* (INB, MO). EL SALVADOR. **Ahuachápan**: San Francisco Menéndez–Tacuba, 0–2 mi. NE of San Francisco Menéndez, 200–450 m, *Croat 42075* (MEXU, MO). GUATEMALA. **Without locality**: *Heyde 463* (US); *Aguilar 309* (F). **Chiquimula**: Río Chiquimula, Santa Bárbara–Petapilla, 4–6 mi. N of Chiquimula, 350–420 m, *Standley 30245* (F); Las Mamacas, 16 mi. S of Guatemala City on CA-9, 3800 ft., *Dziekanowski et al. 3472* (UMO). **Jalapa**: Jalapa–San Pedro Pinula, 1400–1800 m, *Standley 77051* (F). **Jutiapa**: *Standley 75385* (F); *75695* (F); *75212* (F); El Barrial, E of Jutiapan, ca. 800 m, *Standley 75764* (F); Jutiapa–Las Tunas, NW of Jutiapa, 850–900 m, *Standley 76294* (F). **Petén**: 31 km S of Flores, 175 m, *Harmon & Dwyer 2797* (MO); La Libertad, *Lundell 2551* (MICH); 1 km S on old trail to Mahaquila, *Contreras 2912* (LL); Tikal National Park, *Lundell 15292* (LL); *16792* (LL); *Contreras 343* (LL); Dolores, *Contreras 3763* (LL). **Retalhuleu**: Nueva Linda–Chaperico, 120 m, *Standley 87774* (F). **Santa Rosa**: SE of Barberena, 1100–1800 m, *Standley 77740* (F); Cuilapilla, 900 m, *Standley 78087* (F); La Sepultura region, W of Chiquimulilla, 220 m, *Standley 79331* (F); Chiapas, 3500 pp, *Heyde & Lux 3867* (US); Yaxoquintela, floodplain of Río Santa Cruz (upper tributary of Río Usumacinta), 560 m, 16°58′N, 91°47′W, *Rawlins 93* (CM). **Zacapa**: trail between Río Hondo and waterfall, 250–400 m, *Standley 29396* (F); Quebrada

Alejandria, summit of Sierra de Las Minas, Finca Alejandria, 2500 m, *Steyermark 30856* (F); Mpio. Ocozocoautla, E edge of Selva del Ocote, 900 m, *Breedlove 70760* (CAS, MO). HONDURAS. **Colón**: Trujillo, Capuchin Monkey Site West, *Saunders 523* (MO); Bonito Oriental–Limón road, ca. 50 m SW of Río Piedra Blanca, 40 m, 15°46′30″N, 85°41′W, *Evans 1086* (MO). **Copán**: 10 mi. W of Copán, road to La Entrada, 700 m, *Croat 42517* (MO). **Morazán**: Río Yeguare drainage, ca. 14°N, 87°W, *Williams 15908* (F); Río Yeguare, E of El Zamarano, ca. 750 m, *Standley 15448* (F); Río de la Orilla region, SE of El Zamorano, 900–950 m, *Standley 22404* (F). **Olancho**: Juticalpa, 380–480 m, *Standley 17524* (F); Río Olancho, Gualaco–San Bonito Oriental, 7.4 mi. NE of San Esteban, 540 m, 15°20′N, 85°42′W, *Croat & Hannon 64363* (MO). **Yoro**: Río Aguán, Coyoles, *Yuncker et al. 8663* (F, GH, MICH, MO, NY, US); Río Guaymón, La Cieba–San Pedro Sula, SW of Tela, near border of Yoro and Atlántida, 50 m, 15°30′N, 87°43′W, *Croat & Hannon 64666* (MO). MEXICO. *Hahn s.n.* (P). **Campeche**: Yucatán Peninsula, Champoton, *Steere 1742* (CM); Maskall, *Gentle 1186* (CM, MICH, NY); Tuxpena, *Lundell 1074* (F). **Chiapas**: Arriaga–Las Cruces, 5.7 mi., ca. 160 m, *Moore & Bunting 8923* (HB); 51 mi. NE of Chiapas–Oaxaca border on Hwy. 190 to Tuxtla Gutiérrez, 660 m, 16°47′N, 93°18′W, *Thompson et al. 432* (CM, MO); 5 mi. N of Ocozocoautla, along road to Apitpac, 1000 m, *Croat 40544* (MO); Río Cintalapa, Aguas Calientes, Escuintla, *Matuda 18312* (NY); Esperanza, Escuintla, *Matuda 18314* (MEXU, MO); Mpio. Berriozábal, 5 km E of Berriozábal, along Mexican Hwy. 190, 800 m, *Breedlove & Thorne 30412* (MO); Mpio. Ocosingo, Río Usumacinta, 3 km. S of Frontera Corozal, 120 m, *Martínez S. 7309* (MO); Mpio. Ocozocoautla, km 103–104 Hwy. 190, 15.7 mi. E of Cintalapa, 3050 ft., *Bauml & Kimnach 527* (US); Río Grijalva, 10 km S of Hwy. 190 on road to Acala, at Nandaburri, 1600 ft., *Laughlin 2811* (F). **Guerrero**: Acapulco, *Palmer 462* (US). **Oaxaca**: Tuxtepec–Matias Romero, <100 m, *Croat 78724* (CHIP, MO); 7.5 mi. SW of Tuxtepec on road to Valle Nacional, *Moore & Bunting 8908* (HB); 14 mi. N of Puerto Escondido on Rte. 131 to Oaxaca, 300 m, 16°13–47′N, 97°5–8′W, *Thompson et al. 424* (CM, MO); 5 mi. N of Palmar, 54 mi. N of junction of Highways 185 and 190, along Hwy. 185, 65 m, *Croat 40002* (MO); Parque Nacional de Laguna Temazcal, Temazcal, 150 m, 18°25′N, 96°25′W, *Hammel & Merello 15454* (MO). **Quintana Roo**: Mpio. Chetumal, 6.5–7 km N of Tomás Garrido on the road joining Hwy. 186 W of Nicolas Bravo, 150 m, 18°6′N, 89°3′W, *Saunders et al. 9950* (MO); 1 km E of Chanca Veracruz, *E. Cabrera & H. Cabrera 4981* (MEXU). **San Luis Potosí**: Tamazunchale, *Edwards 549* (F, MO). **Veracruz**: Córdoba–Veracruz, Ejido San José de Gracia below Penuela, *Moore & Bunting 8877* (HB); San Lorenzo Tenochtitlán, 22–75 m, *Wing 50* (GH). **Yucatán**: *Schott 489* (BM); Mérida, *Gaumer 489* (BM, F); Izamal, *Gaumer 23174* (F) *Gaumer 1422* (F); *Greenman 376* (F); *Gaumer 23823* (F, US). NICARAGUA. **Boaco**: Las Pitas, Camoapa, 400 m, 12°28′N, 85°35′W, *Moreno 10643* (MO); Río Las Cañas, along Hwy. 33, ca. 3.1 km N of Hwy. 35 intersection, ca. 275 m, 12°38′N, 85°33′W, *Stevens 5838* (MO). **Chontales**: Route 7, 5 km SE of Juigalpa, *Moore 1622* (MO). **Granada**: Laguna de Apoyo, 110–180 m, 11°53′N, 86°01′W, *Moreno 11178* (MO). **Masaya**: Parque Nacional Volcán Masaya, N slope of Volcán Santiago, ca. 375 m, 11°59′N, 86°10′W, *Stevens 5267* (BM, MO); summit of Volcán Masaya, 500 m, *Stevens 2950* (MO); Piedra Quemada, 2 km E of Volcán Masaya, 250 m, *Stevens 4606* (BM, MO). **Matagalpa**: Ranchería, 11 km NE de Muy Muy, ca. 280 m, 12°46′N, 85°31′W, *Moreno 24483* (AAU, MO); Río Yasica, Tuma, ca. 28 km NE Matagalpa, El Diamante, ca. 350–400 m, 13°04′N, 85°46′W, *Guzmán et al. 915* (MO). **Río San Juan**: Boca de Sábalos, "La Toboba," 70–90 m, 11°03–04′N, 84°28–29′W, *Robleto 1833* (US). **Rivas**: Tola–Las Salinas, El Coyol, ca. 2.3 km beyond entrance of Hda. Miramar, ca. 30–40 m, 11°23′N, 85°58′W, *Stevens 9749* (BM, MO). **Rivas–Carazo–Granada**: Río La Pita–Río Escalante, ca. 20 m, 12°34′N, 86°08′W, *Stevens 9718* (BM, MO). **Zelaya**: SW of Puerto Cabezas, 0–2 m, 14°01′N, 83°24′W, *Stevens 7880* (MO); Mpio. Siuna, Wany, *Ortiz 59* (MO). PANAMA. **Canal Area**: Balboa, *Standley 29256* (US); road S-10 N of Escobal, *Croat 12458* (MO, NY, U); Rodman Marine Base, Rodman Naval Ammunition Supply Depot, W of Balboa, 70–80 m, 8°58′N, 79°36′25″W, *Howard 147* (MO); road to Cerro Pelado Radar Station, 0.5 km NW of Gamboa, 75–150 m, *Nee 7760* (MO, RSA); Curundu, Parque Metropolitano, 8°58′N, 79°32′55″W, *Croat & Zhu 76202* (MO); Gamboa, *Croat 74755* (F, MO); Geologic Test Site N of Paraíso, *Croat 12977* (MO); near Summit Hills Golf Course, *Croat 10956* (MO); Gaillard Hwy., vic. Summit Golf Club, 40 m, 9°03′N, 79°37′W, *Croat 69835* (AAU, MO, US); Radar Station Road, 1 mi. N of Summit Gardens, *Croat 9080* (MO); Barro Colorado Island, *Shattuck 115* (F, GH); *Zetek 4675* (MO, US); Wheeler 5, *Shattuck 215* (MO); laboratory clearing, *Croat 10261* (MO); *9259* (MO); Colorado Point, *Croat 6138* (MO); Vista Alegre, *Zetek 5576* (MO); Chagres River, vic. of Juan Mina, Flat Rock, *Bartlett & Lasser 16839* (MICH, MO); Fort Clayton, vic. of end of C-16 road, *Blum 2243* (MO, SCZ); Ft. Sherman, *Standley 31020* (US); Madden Dam Area, Boy Scout Road, *Porter et al. 4062* (MO); Madden Forest, Las Cruces Trail, *Croat 11878* (MO); 140 m, 9°06′20″N, 79°37′20″W, *Croat & Zhu 77072* (MO); Pipeline Road, 2–4 mi. N of Gamboa, ca. 100 m, *Gentry 6543* (MO); Río Cocoli, road K-9, *Stern et al. 348* (GH, MO, US); Paraíso, *Tyson & Lazor 6194* (F). **Coclé**: Penonomé and vic., 50–1000 ft., *Williams 381* (NY). **Darién**: Cerro Pirre region, El Real, *Croat & Porter 15460* (MO); Santa Fe region, Univ. of Georgia Cuipo Forest Site #2, 15 m, *Duke 14258* (F, MO). **Herrera**: Ocú, *Ebinger 1090* (MO, US). **Los Santos**: ca. 5 m S of Las Tablas, *Burch et al. 1236* (MO, UC); Pocrí, *Dwyer 1189A* (MO); Las Tablas, *Dwyer 1189* (MO). **Panamá**: along road to Bique, 5 km SW of Arraiján, 20–40 m, *Nee 7699* (MO, US); Panamá Viejo, *Rose 18505* (NY, US); road K-15 near Huile, vic. Gatún Lake, *Smith et al. 3277* (F, US); El Llano–Chepo, *Gentry & Tyson 1727* (MO, SCZ); Tocumen, *Dwyer 4220* (MO); vic. Macambo, *Croat 14911* (MO); Cerro Campana, *Croat 12018* (MO, SCZ); Penonomé and vic., 50–1000 ft., *Williams 381* (NY); San José Island, Pearl Archipelago, *Erlanson 234* (US); *402* (GH, US); *Johnston 974* (GH, MO), *918* (GH), *12* (GH), *960* (GH).

Philodendron jefense Croat, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, along road short of summit, 550–800 m, 9°15′04″N, 79°30′04W, *McPherson 10038* (holotype, MO–3475849; isotypes, K, PMA, US). Figures 238, 239.

Planta hemiepiphytica; internodia brevia, in sicco usque 3 cm diam.; cataphylla 20–24 cm longa, acute 2-costata, mox decomposita et persistentia ut fibrae pallide brunneae; petiolus teres, 38–76 cm longus, 4 mm

diam.; lamina late ovata, 39–54 cm longa, (22.5)34–49 cm lata, cordata basi, in sicco canoviridis; inflorescentia 1; pedunculus 10–13 cm longus, 4–5 mm diam.; spatha 9.5–14 cm longa, omnino viridis, in sicco cum magnis maculis albis; pistilla (6)7–8-locularia; locules cum 6 seminibus; baccae albae.

Hemiepiphytic; stem appressed-climbing; internodes short, to 3 cm diam.; roots moderately few per node, drying to 3 mm diam., sharply ridged, brown; cataphylls 20–24 cm long, sharply 2-ribbed, persisting, promptly weathering to light brown, semi-organized fibers with small, thin fragments of epidermis persisting; **petioles** 38–76 cm long, 4 mm diam., terete, drying black; **blades** broadly ovate, short acuminate at base, cordate at base, 39–54 cm long, (22.5)34–49 cm wide (0.8–1.4 times longer than wide), (0.5–0.6 times the petiole length), about one-half as long as the petiole, margins sinuate, upper surface glossy, drying gray-green and semiglossy, lower surface glossy, drying minutely granular; anterior lobe 22–25 cm long, 24.5–29.7 cm wide (1.8–2 times longer than posterior lobes); posterior lobes 12–14 cm long, 12.2–13.2 cm wide, obtuse; midrib drying darker than surface above; basal veins 5 pairs per side, first and second free to base, the remainder coalesced 3–6 cm; posterior rib naked to 3–3.5 cm long; primary lateral veins 5–6 per side, departing midrib at a 35–45° angle; minor veins frequently branched, arising from both the midrib and primary lateral veins, minute pustules visible between veins on both surfaces; "cross-veins" many. INFLORESCENCES 1 per axil; peduncle 10–13 cm long, 4–5 mm diam., terete, black-drying; **spathe** 9.5–14 cm long (ca. 1 time longer than peduncle), green throughout, drying with large white flecks; spathe blade 6 cm long; spathe tube 6 cm long; pistillate portion 5 cm long; **spadix** to 11 cm long; staminate portion 5.5–6 cm long, 7–10 mm diam.; fertile staminate portion to 1 cm diam.; sterile staminate portion 7 mm diam.; pistils 3.9 mm long; ovary (6)7–8-locular, locules 3.2 mm long, 0.4–0.5 mm diam., with axile placentation; ovules 2-seriate; funicle 0.3–0.4 mm long, adnate to lower part of partition, style similar to style type D; style apex flat; style boss small. INFRUCTESCENCE with berries white (immature); seeds 6 per locule, 1–1.1 mm long, 0.2–0.3 mm diam., translucent.

Flowering in *Philodendron jefense* is documented by a single collection with immature fruits collected in December. Flowering apparently occurs during the wet season.

Philodendron jefense is endemic to Panama on Cerro Jefe in *Premontane rain forest* at about 800 m elevation.

Philodendron jefense is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Reticulata*. This species is distinguished by its appressed-climbing habit, short, thick internodes, sharply 2-ribbed cataphylls promptly weathering to light brown, semi-organized fibers with small, thin fragments of epidermis persisting, terete petioles (about twice as long as the blades), broadly ovate, gray-green-drying blades, and solitary long-pedunculate inflorescences with the spathes green outside.

Philodendron jefense is probably closest to *P. lazorii* Croat, which shares broadly ovate, gray-green-drying leaf blades and semi-organized, brownish masses of persistent cataphyll fibers. The latter species differs in having matte-drying blades with the lower surface smooth and minutely brownish- or whitish-speckled, with the minor veins drying darker than the surface and weakly puckered without any sign of branching or cross-veins. In contrast, *P. jefense* has blades semiglossy on drying with the lower surface sparsely granular with frequently branched minor veins and with cross-veins not drying darker than the surface. The upper surface lacks any signs of raphide cells.

The species name refers to the type locality, Cerro Jefe, which has proven to be one of the most endemic-rich areas for its size of any site in Panama.

Philodendron jodavisianum G. S. Bunting, Gentes Herb. 9: 337. 1965. TYPE: Mexico. Chiapas: Cerro de Madrugal, along Teapa–Tacotalpa (Tabasco) Highway, at km 4, W of hwy., on rock face of steep slopes, *Bunting 1526* (holotype, US). Figures 243, 245–248, 253.

Usually hemiepiphytic, terrestrial; stem appressed-climbing, gray-green to brown or green, sap sweet-scented, drying blackened, leaf scars conspicuous, 2 cm long, 1.7 cm wide; internodes weakly flattened on one side, 2-ribbed, weakly glossy, to 8 cm long, but surely longer than wide and 2.5–3 cm diam. at apex, dark to medium green, soon gray, epidermis brown, flaking, fissured sometimes; roots whitish, few per node; cataphylls 10–20 cm long, bluntly or sharply 2-ribbed or unribbed, sharply D-shaped, somewhat spongy, light to medium green or reddish to brownish, sometimes streaked pinkish, semiglossy, drying brown, persisting semi-intact as pale fibers at upper nodes, disorganized below; **petioles** (18)29–91 cm long, (2)3–7(8–12) mm diam., sometimes terete, usually D- or U-shaped, spongy or firm, dark green, flattened or somewhat sulcate to convex, often with medial rib, margins raised adaxially, rounded abaxially, surface semiglossy, minutely and short-lineate; **blades**

triangular-ovate, ± subcoriaceous, moderately bicolorous, long acuminate at apex, deeply cordate at base, 25–74 cm long, 18–34 cm wide (1.1–2.8 times longer than wide), (0.5–2 times longer than petiole), broadest ± near the middle, upper surface dark green, drying blackish, semiglossy, lower surface pale green to yellow-greenish, drying blackish, glossy to semiglossy or matte; anterior lobe 18–58 cm long, 10.1–40.4 cm wide (1.7–4.3 times longer than posterior lobes); posterior lobes 8–17 cm long, (3.7)5–17 cm wide, obtuse to rounded; midrib broadly sunken to broadly convex or flat, dark green above, raised to narrowly convex, thicker than broad, concolorous or darker than surface below; basal veins 5–10 per side, in part coalesced to 4 cm, barely naked or naked to 2 cm; primary lateral veins 7–11 per side, departing midrib at a 50–60° angle, ± straight to the margins, obtusely to weakly or narrowly sunken and sometimes weakly quilted above, convex and darker than surface below; interprimary veins almost as prominent as primary lateral veins; minor veins in part discontinuous and darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2–6 per axil; peduncle 3–13 cm long (to 20 cm long in South America), 2–6 mm diam., pale green to whitish, with raised, prominent white striations; **spathe** semiglossy, 6–14.5 cm long (0.9–3 times longer than peduncle), sometimes greenish with short white lineations throughout; spathe blade white to pale green (at anthesis), reddish (post-anthesis) (B & K red-purple 7.5/7), short-lineate outside (opening 4.6 cm long, 3.6 cm wide), very pale green to white, matte, few, sparse, dark-lineate inside; spathe tube semiglossy and greenish to greenish brown or reddish (maroon or reddish at anthesis) outside, green to white inside; **spadix** weakly exserted from the spathe, 7.6–9.2 cm long, constricted near base of fertile staminate portion; pistillate portion pale green or whitish, cylindrical, 1.4–2.4 cm long, 1 cm diam. at apex, 1.1 cm diam. at middle; staminate portion 5.3–7.6 cm long; fertile staminate portion creamy white, cylindrical to weakly tapered, 0.85–1.5 cm diam. at base, 0.7–1.3 cm diam. at middle, 6–10 mm diam. ca. 1 cm from apex, broadest at the base, narrower than the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the apical area of the pistillate portion, gray-white, 1.1–1.5 cm diam.; pistils 1.8–2.5 mm long, 1–1.4 mm diam.; ovary 4–6(5–7)-locular; locules 1.3–1.7 mm long, 0.5–0.7 mm diam., with axile placentation; ovules 18–26(23–28) per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style 0.2–0.3 mm long, 1–1.4 mm diam., similar to style type B; style apex flat to slightly rounded; stigma subdiscoid, brushlike, unlobed, 1–1.3 mm diam., 0.2–0.6 mm high, covering entire style apex; the androecium truncate, margins 4–6-sided; thecae oblong to obovate, 0.3–0.5 mm wide, ± parallel to one another, contiguous; sterile staminate flowers blunt, 1.6–1.8 mm long, 1.4–1.5 mm wide. INFRUCTESCENCE with berries white (mature), 6 mm long, 2.6 mm diam.; seeds 14–16(24–28) per locule, 1.3–1.7 mm long, 0.2–0.3 mm diam. JUVENILE plants with internodes 8 cm long, 5 mm diam.; petioles sharply U-shaped in cross section, usually lacking medial rib adaxially, margins erect.

Flowering in *Philodendron jodavisianum* occurs in the late dry season and throughout much of the rainy season (April through October) in Panama. In Costa Rica it has been collected in flower in February, and post-anthesis collections have been made in January. Immature fruits have been collected August through November.

Philodendron jodavisianum ranges from southern Mexico to Colombia, Ecuador, and Venezuela (Mérida) from near sea level to 1500 m elevation. It occurs in *Tropical wet forest* and *Premontane wet forest* in Panama and Costa Rica but also in *Tropical moist forest* in some parts of Central America.

Philodendron jodavisianum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa*. This species is characterized by its short internodes, sharply 2-ribbed cataphylls persisting as pale fibers, petioles flattened or somewhat sulcate above and usually with a medial rib, usually triangular-ovate, blackish-drying blades with many impressed primary lateral veins, and spathes usually greenish on the tube and white on the blade.

Philodendron jodavisianum is quite variable throughout its range, and the type (being one of the most northerly collections) differs from most in having more elliptic blades.

Philodendron jodavisianum is most easily confused with *P. grandipes*, which differs in comprising terrestrial plants with broadly ovate leaf blades. It has also been confused with *P. panamense* K. Krause, which differs in having subterete petioles, promptly deciduous cataphylls, and longer peduncles often bent beneath the spathe (see *P. panamense* for additional details).

Similar collections from South America, especially *Croat 57441* from Bahía Solano, Chocó Department, Colombia, differ in sometimes having distinct "cross-veins." Collections from Pichincha Province, Ecuador (*Croat 55737* and *Grayum & Zamora 9431*), differ in having peduncles 16–20 cm long.

Two Darién collections (*Hammel et al. 16252* and *McPherson 11517*) are unusual in having leaf blades with somewhat flaring posterior lobes and markedly

concave margins. However, the leaves on the second sheet of the McPherson collection are typically shaped with a convex blade margin.

Additional specimens examined. BELIZE. **Toledo**: Blue Creek, *Whitefoord 3234* (BM). COSTA RICA. **Alajuela**: Los Ensayos, Buena Vista de San Carlos, *Barquero 10* (UC); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, *Croat 43583* (MO); Reserva Biológica Monteverde, along Río Peñas Blancas, 820 m, 10°21′N, 84°40′W, *Bello & Haber 2881* (INB, MO); Río Zapote, 5 km S of Canalete, along new road to Upala, 100–200 m, 10°48′N, 85°02′W, *Burger & Baker 9961* (F, MO, SEL); Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36279* (MO); San Ramón, *Bittner & G. Herrera 2134* (CR). **Cartago**: Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36648* (MO); along Camino Raiz de Hule, SE of Platanillo, 1200–1400 m, *Croat 36756* (MO); Jicotea Valley, Jicotea–Río Pacuare, *Croat 36539* (MO). **Guanacaste**: slopes of Miravalles, above Bijagua, ca. 1500 m, *Gómez 19048* (MO). **Heredia**: 11 km E of Cariblanco, 1060 m, *Loiselle 255* (MO); Paracito–Río Claro, Bajo La Hondura, 1100–1400 m, *Croat 44516* (MO); Parque Nacional Braulio Carillo, 1000 m, 10°16′38″N, 84°04′57″W, *Boyle 1285* (MO); Zona Protectora "La Selva," along trail from main road across Quebrada Cantarrana to Río Guácimo, 300 m, *Grayum & Schatz 3216* (DUKE); La Selva Field Station, ca. 100 m, *Croat 44300* (MO); 100–150 m, *44320* (MO); *Grayum 1915* (MO); *Jiménez V* (MO); *Murrell 1710* (DUKE); Río Frío, W of Finca Zona Nueve, ca. 110 m, 10°18′N, 83°53′W, *Grayum 3562* (MO); Río Sucio, near Puerto Viejo, 2 m, *Croat 35703* (MO). **Limón**: Manzanillo de Talamanca, ca. 5 m, 9°38′N, 82°39′W, *Grayum & Burton 4340* (MO); ca. 11 mi. S of Siquirres, 650 m, *Croat 43329* (MO); Cerro Coronel, 10–40 m, 10°40′N, 83°40′W, *Stevens 24346* (MO); Río Sixaola, ca. 0.5 mi. SW of Bambú, ca. 3 mi. NE of Bratsi, ca. 15 m, *Croat 43254* (MO). **Puntarenas**: ca. 1 km S and 2 km W of Cañasas, 60 m, 8°34′N, 83°25′W, *Croat & Grayum 59807* (CM, CR, K, MO); Osa Península, 200 m, *Aguilar 2201* (CR, INB); Golfo Dulce Forest Reserve, Rancho Quemado, 200 m, 8°42′N, 83°33′W, *Hammel & Robles 16834* (CR, MO); Piedras Blancas, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67696* (CR, MO); *67693* (CR, F, MO); Golfito, *G. Herrera & Rivera 7042* (CR). **San José**: above Río Sucio, 5–6000 m, *Pennington et al. 11529* (K); San Isidro del General–Dominical, SW of San Isidro, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35253* (CR, F, MO); 9 mi. SW of Río Pacuar, 680 m, *Croat 35344* (MO); Carara Reserve, SW part of Montañas Jamaica, ca. 2.5 km NE of Bijagual de Turrubares, 460–520 m, 9°45′N, 84°33′30″W, *Grayum et al. 5488* (MO); vic. of San Isidro El General, 900 m, *Molina et al. 18063* (EAP, F, GH, NY, UC, US); Puriscal, Z.P. La Cangreja, 800 m, *Morales 2020* (CR, INB); Tarrazú, vic. Hormiguero, 1100–1200 m, *Croat 78962* (INB, MO). GUATEMALA. **Alta Verapaz**: Tucurú–El Estor, 4–9 mi. up road to Oxec, gravel road N off Hwy. 7E, ca. 6 km NE of Panzós, 500–800 m, *Croat 41607* (MO); *41698* (K, MO, NY). **Izabal**: 12 km NW of El Estor, 650 m, *Martínez & Stevens 23305* (MO). HONDURAS. **Atlántida**: Lancetilla Botanical Gardens, 2 mi. WSW of Tela, 10–150 m, *Croat 42640* (K, MO); 70–90 m, 15°44′N, 87°27′W, *Croat & Hannon 64612* (CM, CR, EAP, G, MEXU, MO); Lancetilla, 100 ft., *Yuncker 5008* (F, MICH, MO, NY). MEXICO. **Tabasco**: Mpio. Teapa, 7 km SE of Teapa on road to Tacotalpa, Rancho San Eneas, 70 m, 17°35′N, 92°50′W, *Hammel & Merello 15516* (MO). NICARAGUA. **Chontales**: 4 km NNW of Cuapa, Cerro Oluma, 700–775 m, 12°18′N, 85°23′30″W, *Nee 28413* (MO, NY). **Río San Juan**: Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill & Vincelli 3623* (MO); Río Indio, 5 hours upriver from San Juan del Norte, 11°07′N, 83°50–52′W, *Riviere 247* (MO). **Zelaya**: ca. 6 km upriver from Barra de Punta Gorda, 8–10 m, 11°30′N, 83°49′W, *Stevens 20756-a* (MO); Mpio. Siuna, Santa Rosa, *Ortiz 67* (MO). PANAMA. **Bocas del Toro**: Escudo de Veraguas Island, N coast, 5 m, 9°05′N, 81°35′W, *McPherson 11412* (MO, US); Fortuna Dam area, road along Continental Divide, 2.8 mi. S of Continental Divide, 850–950 m, 8°45′N, 82°15′W, *McPherson 9676* (MO, US); Chiriquí Grande–Fortuna, 1.2 mi. N of Divide, 5.3 mi. N of bridge over Fortuna Dam, 910 m, 8°44′N, 82°17′W, *Croat 60450* (MO, PMA, RSA); along Divide, 1.1 mi. W of highway, 1200 m, 8°44′N, 82°17′W, *Croat 60368* (MO); E of camp Corriente Grande (IRHE), 200 m, *Correa et al. 3697* (PMA). **Chiriquí**: Río Chiriquí Valley, vic. of Fortuna Dam, 1100–1200 m, 8°45′N, 82°18′W, *Croat 66587* (F, IBE, M, MEXU, MO, US); 1000–1200 m, 8°45′N, 82°15′W, *Correa et al. 2686* (MO, PMA); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60080* (CM, MO); Gualaca–Fortuna, 10 mi. NW of Los Planes de Hornito, 1260 m, 8°45′N, 82°17′W, *Croat 50074* (MO); Gualaca–Chiriquí Grande, Río Hornito, ca. 0.5 km S of Centro de Científicos, 1010–1130 m, 8°44′N, 82°13′30″W, *Croat 67922* (MO); 8°45′N, 82°18′W, *Croat & Zhu 76376* (MO, SEL); 1100–1200 m, 8°45′N, 82°15′W, *Thompson 5026* (CM); Río Chiriquí, beyond Gualaca, 10.8 mi. beyond Los Plantes de Hornito, ca. 1400 m, *Croat 48721* (MO). **Coclé**: Santa Rita Ridge Road, 4–6 km from Transisthmian Highway, 150–200 m, *Croat 34280* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76960* (MO); El Copé region, near Continental Divide, ca. Mile 1.5, ca. 900 m, *Croat 44572* (MO); ca. Mile 5.6, 800 m, *Croat 75068* (MO); La Pintada–El Copé, 3000 ft., *Hammel 2633* (MO); El Valle region, N of El Valle de Antón, La Mesa, 900–1000 m, 8°40′N, 80°10′W, *Hamilton et al. 4111* (INB, MO); 800–900 m, 8°38′N, 80°09′W, *Croat 67122* (CAS, CM, COL, HNMN, L, MEXU, MO, PMA); 860–900 m, *37396* (MO); *67211* (AAU, DUKE, MO, NY, PMA, TEX); *67213* (AAU, CM, EAP, MO, PMA, TEX, USCG); *67121* (F, HNMN, MO); *67129* (AAU, CAS, CM, COL, CR, F, HUA, K, L, MEXU, MO, NY, P, PMA, SEL, TEX); 775 m, 8°36′N, 80°07′W, *74793* (KUN, MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76742* (MO, SEL); *76710* (MO). **Colón**: Río Guanche, ca. 3–5 mi. inland, 10–100 m, *Croat 26175* (MO). **Darién**: Cerro Pirre region, Alturas de Nique region, S of El Real, near Cana mine, 650–800 m, 7°45′N, 77°40′W, *McPherson 11526* (MO); *11517* (B, MO); Cana gold mine, 480 m, *Croat 38003* (MO); *38039* (MO); 600–100 m, *Croat 37743* (MO); Parque Nacional Darién, N of Tacarcuna, ca. 18 km E of Pucuro, 600–800 m, 8°05′N, 77°16′W, *Hammel et al. 16481* (MO); ca. 17 km E of Pucuro, 850 m, 8°03.5′N, 77°17′W, *16252* (MO). **Panamá**: El Llano–Cartí road, 10 m from highway, near El Llano, 330 m, *Croat 33779* (F, MO, NY); Mile 5–6, 350–375 m, *34771* (F, MO); Mile 6.8, 350 m, *49128* (AAU, CAS, CM, MEXU, MO); Mile 10.1, 325–350 m, *67366* (MO); Río Majé–Quebrada Brava, ca. 60 m, *Croat 34657* (F, MO); Cerro Campana, *Croat 25252* (MO); *25204* (MO); along trail to summit, 780–875 m, *Croat 17207* (F, MO, NY); at end of road beyond Su Lin Hotel, *Croat 14227* (MO); 800 m, 8°41′N, 79°56′W, *74772* (CM, MO); summit and upper trail, *Witherspoon & Witherspoon 8462* (MO); ca. 1 mi. from highway, 450 m, *Croat 35950* (MO, PMA); Cerro Jefe region, Campo Tres, ca. 700 m, *Croat 27064* (F, MO); 700–750 m, 9°15′N, 79°25′W, *Croat 68687* (IBE, MO, TEX). **San Blas**: El Llano–Cartí, 23–29 km from Pan-American Highway, 300–400 m, 9°22′N, 78°69′W,

Knapp 1839 (MO, PMA); El Llano–Cartí Road, vicinity Nusagandi, 300–350 m, 9°15′N, 79°W, *Croat 69279* (DUKE, MO); 300 m, 9°20′N, 79°W, *Croat & Zhu 76542* (MO); 350 m, 9°20′N, 79°W, *Croat & Zhu 77011* (MO); 450 m, 9°18′N, 79°59′W, *Croat 75121* (MO). **Veraguas**: Río Concepción–Río Barrera, 300–600 ft., *Hammel 5252* (MO); Santa Fe region, Alto Piedra–Calovébora, 0.5 mi. N of Escuela Alto Piedra, Parque Nacional Cerro Tute, 800–1030 m, *Croat & Zhu 76914* (MO); 5–8 km from school, 730–770 m, *Croat 25967* (MO); Río Primero Brazo, 5 mi. NW of Santa Fe, 700–1200 m, *Croat 23114* (MO); 15.6 km NW of Santa Fe, 450–550 m, *Croat 27639* (MO); 0.6 mi. beyond Escuela Agrícola Alto Piedra, 730 m, *Croat & Folsom 33997A* (MO); *34062* (MO); ca. 1200 m, 8°32′N, 81°07′W, *Hamilton et al. 1280* (MO); Escuela Agrícola Alto Piedra, *Mori & Kallunki 2529* (MO); Santa Fe–Río San Luis, past Escuela Agrícola Alto Piedra, Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66901* (CM, MO).

Philodendron knappiae Croat, sp. nov. TYPE: Panama. Chiriquí: Cerro Hornito, in elfin forest on ridges and summit, approached from Los Planes de Hornito, 2100 m, 8°42′N, 82°06′W, 14 Mar. 1982, *Knapp, Kress & Hammel 4219* (holotype, MO–3043611). Figures 240, 244, 249, 254.

Planta terrestris aut hemiepiphytica; internodia 0.5–7 cm longa, 1–1.7 cm diam., in sicco brunnea; cataphylla 10–18 cm longa, acute 2-costata, sulcata adaxialiter, viridia, deciduа; petiolus obtuse D-formatus, 14–19 cm longus, in sicco 2–7 mm diam.; lamina ovato-triangularis, cordata basi, 16–23.5 cm longa, 7.5–11.5 cm lata; inflorescentia 1; pedunculus 2–3 cm longus, 5–6 mm diam.; spatha 7–8 cm longa, extus viridis, intus subrosea; pistilla 4-locularia; loculi 4-ovulati.

Terrestrial or hemiepiphytic; stems usually erect; internodes short, somewhat flattened on one side with marginal ribs, moderately glossy, 0.5–7 cm long, 1–1.7 cm diam., longer than broad below, short near apex, medium green, epidermis smooth, light brown; cataphylls 10–18 cm long, sharply 2-ribbed, green, sulcate adaxially, margins weakly raised abaxially, deciduous; **petioles** 14–19 cm long, 2–7 mm diam., bluntly D-shaped, green, tinged reddish; **blades** ovate-triangular, subcoriaceous, bicolorous, long-apiculate at apex, cordate at base, 16–23.5 cm long, 7.5–11.5 cm wide (1.8–3 times longer than wide), (1.1–1.4 times longer than petiole), about equal in length to petiole, upper surface semiglossy, drying dark brown, lower surface slightly paler, drying dark yellow-brown or dark yellow-green; anterior lobe 12–18.5 cm long, 10.6–13 cm wide (2.2–3.3 times longer than posterior lobes); posterior lobes 5–8 cm long, 5–6.5 cm wide (1.4–1.8 times longer than wide), narrowly to obtusely rounded; sinus hippocrepiform, 3–5.5 cm deep; midrib broadly convex, paler than surface above, convex, reddish or paler than surface below; basal veins 3(5) per side, with 0–1 free to base, 2–3 coalesced 1–1.5 cm; posterior rib naked; primary lateral veins 5–7 per side, departing midrib at a (40)55–70° (lowermost to 80°) angle, arcuate-ascending to the margins, weakly visible above, weakly raised, often reddish below; minor veins distinct below, arising from the midrib only; secretory ducts present but inconspicuous. INFLORESCENCES 1 per axil; peduncle 2–3 cm long, 5–6 mm diam.; **spathe** 7–8 cm long (2.3–3.6 times longer than peduncle), weakly constricted above the tube, 1.5 cm diam. at constriction, green throughout, pinkish within; spathe tube 3–4 cm long, 1.9 cm diam.; **spadix** 5.5–7 cm long, white throughout; pistillate portion 1.2 cm long, 1 cm diam.; staminate portion 4.3–5.8 cm long, 8–12 mm diam.; pistils 1–1.3 mm long, 0.7 mm diam.; ovary 4-locular; locules 0.8 mm long, 0.3–0.4 mm diam., with axile placentation; ovules 4 per locule, 2-seriate, 0.2 mm long, longer than funicle; funicle 0.1 mm long, adnate to lower part of partition, style similar to style type B; style apex flat to concave; stigma ± hemispheroid, unlobed, 0.8 mm diam., 0.2 mm high, covering entire style apex; the androecium truncate, ± prismatic, margins irregularly 4–6-sided, mostly 4–5-sided, 0.8–1.1 mm long; thecae oblong, 0.4 mm wide, ± parallel to one another, not contiguous; sterile staminate flowers irregularly 4–6-sided, 0.9–1.1 mm long.

Flowering in *Philodendron knappiae* apparently occurs in the dry season and is documented by only two fertile collections, one flowering and one post-anthesis, both made in March.

Philodendron knappiae is endemic to western Panama, known only from the type locality in Chiriquí Province on Cerro Hornito in *Tropical Lower Montane rain forest* at 2100 m elevation.

Philodendron knappiae is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is recognized by its relatively small stature; short internodes (distally) with smooth, brown epidermis; adaxially sulcate, sharply two-ribbed, green but densely short-red-lineate, deciduous cataphylls; bluntly D-shaped petioles (about as long as the blades); small, ovate-triangular dark brown-drying blades with a hippocrepiform sinus; and solitary inflorescences with the spathe green outside and pink inside.

The species is perhaps most easily confused with *P. wilburii*, which has leaf blades of similar size and shape. The latter species differs in having longer internodes drying with a tan, glossy epidermis, thicker blades drying yellowish green to dark olive brown above, 2–3 inflorescences per axil, and 2 ovules per locule (vs. 4 per locule for *P. knappiae*).

Additional specimens examined. PANAMA. **Chiriquí**: Cerro Hornito, above Los Planes de Hornito, 1750 m, 8°41′N, 82°10′W, *Croat 67982* (CM, MO); 2100 m, *Kress et al. 82-1363* (DUKE).

Philodendron lazorii Croat, sp. nov. TYPE: Panama. Canal Area: vic. Madden Lake, along both sides of stream SSE of pumping station (SE of dam), 140 m, 9°13′N, 79°37′W, 18 Jan. 1990, *Croat 69833* (holotype, MO–3789003–5; isotypes, AAU, B, CAS, CM, COL, CR, F, GH, K, MEXU, NY, PMA, QCNE, RSA, SCZ, TEX, US, VEN). Figures 13, 14, 250–252, 255–258.

Planta hemiepiphytica; internodia 1–4 cm longa, 5 cm diam.; cataphylla acute D-formata, persistentia semi-intacta nodis superioribus, demum decidua; petiolus teres, 37–63(76) cm longus, 5–6 mm diam.; lamina late ovata, 32–54 cm longa, (22)34–49 cm lata, cordata basi, in sicco canoviridis; sinus hippocrepiformis vel obovatus; inflorescentia 2; pedunculus 8.6–17 cm longus; spatha 12–13.5 cm longa; pistilla (4)5–6-locularia; loculi 10–14(18)-ovulati.

Hemiepiphytic; stem appressed-climbing (scandent as juvenile); internodes weakly striate, 1–4 cm long, 5 cm diam., ± broader than long, light olive-green to dark yellow-green, glossy, roots 1–3 per node, dark brown to reddish brown, matte, smooth to densely scaly, to 30 cm or longer, 3–5 mm diam., feeder roots to 8 mm diam., densely scaly; cataphylls 17–19 cm long, pale yellow-green, sharply D-shaped, margins acutely raised, persisting semi-intact at upper nodes with a dense reticulum of coarse fibers, often overlain with a thin, fragmented epidermis, becoming dilacerated, eventually deciduous; **petioles** 37–63(76) cm long, 5–6 mm diam., terete, dark green, firm, flexible, surface matte, faintly dark green striate; **blades** broadly ovate, subcoriaceous, long-acuminate at apex, cordate at base, 32–54 cm long, (22)34–49 cm wide (0.97–1.4 times longer than wide, averaging 1.13 times), (0.65–0.9 times the petiole length), slightly shorter in length than petiole, upper surface dark green, drying gray-green, weakly to semiglossy, lower surface drying gray-green, matte, much paler; anterior lobe 27–33 cm long, 36 cm wide (1.6–2.2 times longer than posterior lobes); posterior lobes 13–17 cm long, 16–19.5 cm wide, obtuse; sinus hippocrepiform to obovate, 9.5–11.5 cm deep; midrib flat to broadly raised, concolorous to slightly paler than surface above, narrow-rounded to bluntly acute, darker than surface below; basal veins (5)6–7 per side, with 0–1 free to base, 3rd and higher order veins coalesced 2–4.5 cm, obscure; posterior rib 2–3 cm long along the sinus; primary lateral veins 3–4 per side, departing midrib at a 40–50° then to 70° angle, straight to weakly arcuate to the margins, weakly and obtusely sunken and concolorous or paler above, convex and darker than surface below; minor veins moderately distinct, arising from both the midrib and primary lateral veins, drying weakly puckered and darker than surface below, upper surface usually drying with whitish cells visible, lower surface drying smooth and minutely brownish to whitish speckled. INFLORESCENCES 2 per axil; peduncle 8.6–17 cm long, to 1.1 cm diam., medium green, lightly white-striate, heavily white-striate nearest apex; **spathe** 12–13.5 cm long (spathe equal in length to or slightly shorter than peduncle), constricted above the tube, 2.9 cm diam. at constriction, margins pale to creamy; spathe blade yellowish green outside, 8 cm long (opening 4 cm wide), creamy on outer margins, glossy inside; spathe tube medium green, finely white-striate with pale margins outside, 5 cm long, 3.3 cm diam., pale yellowish green, glossy inside; **spadix** bluntly pointed at apex, 10.9–11.3 cm long, constricted 1.5 cm above base of fertile staminate portion; pistillate portion pale yellowish green, 3.3–4 cm long, 1 cm diam. at base, 1.5 cm diam. midway, 1.4 cm diam. at apex; staminate portion 7.8–9.3 cm long; fertile staminate portion creamy white, 1.7 cm diam. at middle, 11 mm diam. ca. 1 cm from apex; sterile staminate portion barely detectable, creamy white, drying darker than fertile staminate flowers, 1.7 cm diam.; pistils 1.9–2.5 mm long; ovary (4)5–6-locular, 1.1 mm diam., locules 1.1–1.6 mm long, 0.3–0.4 mm diam., with axile placentation; ovules 10–14(18) per locule, 2-seriate, 0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style 0.9 mm diam., similar to style type D; style apex ± rounded to bluntly pointed; style boss broad and pronounced; stigma subdiscoid, unlobed, ± truncate, 1.5 mm diam., 0.3 mm high, covering entire style apex, depressed shallowly and medially; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.7–1 mm long; thecae oblong, 0.4–0.5 mm wide, not contiguous, ± parallel to one another; sterile staminate flowers irregularly 4–6-sided, slightly clavate to prismatic, 1.2–1.9 mm long. JUVENILE plants with internodes matte, gray-green, 6 cm long, 7 mm diam.; petioles terete; blades weakly velvety; upper surface ± glistening-glossy, lower surface matte, much paler, with flecks of brilliance; minor veins very distinct, darker than surface.

Flowering in *Philodendron lazorii* occurs in the late dry season and early rainy season (March through June), with mature fruits in August. Immature fruits have been collected in March and June, which indicates that there must be flowers in the late wet season as well (or perhaps it indicates bimodal flowering).

Philodendron lazorii is endemic to Panama, known from the type locality, a region of limestone outcrops near Madden Lake, at about 100 m elevation in *Tropical moist forest,* and in Darién Province at 250 to 1050 m in *Tropical moist forest* and *Premontane wet forest.*

Philodendron lazorii is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its thick, short internodes, cataphylls persisting semi-intact with an organized network of yellow-brown fibers, terete petioles averaging 1.25 times longer than the blade, and broadly ovate, gray-green-drying blades matte on the lower surface.

Philodendron lazorii is probably most closely related to *P. panamense,* which has similar inflorescences. The latter species differs in having semiglossy, ovate-triangular blades usually 1.3 or more times longer than wide (averaging 1.5 times longer than wide), and petioles commonly shorter than the blade. In addition, it has generally shorter peduncles (usually shorter than the spathe).

This species is also similar to *P. jefense.* See that species for a discussion of the differences.

Philodendron lazorii is named in honor of one of its original collectors, Robert Lazor (Army Corps of Engineers, Vicksburg), who collected in Panama while a student at Florida State University.

Additional specimens examined. PANAMA. **Canal Area**: Madden Lake Cave area, ca. 9°13′N, 79°37′W, *Tyson & Lazor 6266* (FSU, IBE); Salvador Hill, near Juan Mina, *Bartlett & Lasser 16785* (MICH, MO). **Darién**: along trail from base camp to Rancho Frío on slopes of Cerro Pirre, 200–450 m, 7°58′N, 77°43′W, *Croat & Zhu 77126* (CAS, CM, CR, MO); W side of Cerro Pirre, 800–1050 m, 7°56′N, 77°45′W, *Croat 68953* (DUKE, HUA, M, MO).

Philodendron lentii Croat & Grayum, sp. nov. TYPE: Panama. Coclé: El Valle region, between Finca Mandarinas and Finca Furlong, ca. 1 km off road, vic. La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, 11 June 1987, *Croat 67163* (holotype, MO–3582921; isotypes, AAU, B, BR, CAS, CM, COL, CR, CUVC, DUKE, EAP, F, G, GH, HMNM, HUA, IBE, K, MEXU, NY, P, PMA, QCA, RSA, S, SCZ, TEX, US, VEN). Figures 259–265.

Planta hemiepiphytica; caulis scandens; internodia 4–12 cm longa, 1.5–4.5 cm diam.; cataphylla 20–23(40) cm longa, plerumque incostata, interdum 1–2 costata, decidua; petiolus teres vel late D-formatus, interdum late sulcatus, 22–44 cm longus, 4–12 mm diam.; lamina ovato-cordata, 21.6–51 cm longa, 9–25 cm lata, truncata vel subcordata basi; nervis basalibus 1–3(4) utroque, liberis basi; inflorescentia 1–2; pedunculus 3–10 cm longus; spatha 12–21 cm longa, lamina spathae extus viridalba vel alba, intus atrimarronina vel creamea; tubo spathae extus albo vel viridalbo, interdum suffuso subroseo, intus atrimarronino vel violaceipurpureo; pistilla (5)6–8-locularia; loculi (1–2)4–6-ovulati; baccae aurantiacae.

Hemiepiphytic; stem scandent, creeping, assurgent, sap soapy-scented; internodes elongate, semiglossy to matte, 4–12 cm long, 1.5–4.5 cm diam., usually slightly longer than broad, medium to dark green, conspicuously pale striate at upper edge of each node, drying brownish, often narrowly ribbed (ribs irregularly ridged, sometimes warty), epidermis weakly fissured transversely; roots moderately few, to ca. 30 cm long, drying to 2 mm diam., reddish brown; cataphylls 20–30(40) cm long, usually unribbed, sometimes 1-ribbed, sharply 1-ribbed, or weakly to sharply 2-ribbed, greenish, tinged reddish, deciduous, intact; **petioles** 22–44 cm long, 4–12 mm diam., terete to broadly D-shaped, firm, dark green, sometimes purplish below, broadly sulcate, flattened or broadly convex adaxially, convex abaxially, with adaxial margins obtuse to rounded, surface semiglossy, densely and minutely white or dark striate-lineate; **blades** ovate to narrowly ovate or ovate-elliptic, coriaceous to subcoriaceous, conspicuously bicolorous, acuminate to narrowly acuminate at apex, rounded to truncate or subcordate at base, 21.6–51 cm long, 9–25 cm wide (1.4–2.7(3.3) times longer than wide), (0.7–1.4(2.25) times longer than petiole), usually about equal in length to petiole, upper surface dark green, semiglossy, drying dark grayish brown to yellowish brown, lower surface semiglossy to matte, paler; anterior lobe 28–45.5 cm long, 9–25 cm wide (4.9–10.2 times longer than than posterior lobes); posterior lobes 3–7 cm long, broader than long, broadly rounded to obtuse; sinus ± V-shaped to arcuate, to 4 cm deep; midrib flat to broadly convex, paler than surface above, convex, tinged reddish or darker than surface, drying minutely granular below; basal veins 1–3(4) per side, with all free to base; primary lateral veins 8–14 per side, departing midrib at a 60–70° angle, weakly arcuate, ascending to the margins, weakly to narrowly sunken or weakly quilted, drying paler than surface, raised along the margins with the center collapsed (forming a channel) above, convex to weakly raised or weakly pleated, darker than surface, drying minutely granular, paler than surface below; interprimary veins weakly sunken or obscure above, visible below; minor veins visible, few, darker than surface, arising from both the midrib and primary lateral veins, minutely etched in upper surface of fresh leaves, drying raised. INFLORES-

CENCES 1–2 per axil; peduncle 3–10 cm long, 3–7(14) mm diam., pale green; **spathe** 12–21 cm long (1.5–3.98(4.5–5.1) times longer than peduncle), margins reddish; spathe blade greenish white to white outside, 4 cm diam., dark maroon to cream inside; spathe tube white to greenish white, sometimes tinged pinkish or red, densely white-lineate outside, 6–9 cm long, dark maroon to violet-purple, densely white-lineate inside; **spadix** sessile; pale greenish to white throughout, cylindrical, tapered, 11–14(18) cm long, broadest near the base or slightly above the middle, constricted below the middle; pistillate portion green, cylindrical to ovoid-tapered, 6.6 cm long in front, 4.5 cm long in back, 1.1 cm diam. at apex, 1.3–1.4 cm diam. at middle, 8–11 mm wide at base; fertile staminate portion greenish white, tapered to clavate or cylindrical, 6.8–9.4 cm long, 9–16 mm diam. at base, 9–15 mm diam. at middle, 8–10 mm diam. ca. 1 cm from apex, broadest at or near the base, broader than the pistillate portion, sterile staminate portion not detectable; pistils 1.6–2.4 mm long, 1–1.8 mm diam.; ovary (5)6–8-locular; locules 1.2–2 mm long, 0.3–0.6 mm diam., ovule sac 0.8–1.5 mm long, with basal or sub-basal placentation; ovules (1–2)4–6 per locule, 1- or 2-seriate, 0.3–0.5 mm long, longer than or equal in length to funicle; funicle 0.1–0.4 mm long (can be pulled free to base); style 0.1–0.5 mm long, 1–1.6 mm diam., similar to style type B; style apex flat or weakly rounded; stigma discoid, brushlike, unlobed, 1–1.3 mm diam., 0.1–0.2(0.6) mm high, covering almost entire style apex or just the center of style apex; the androecium truncate, margins 4–6-sided (4–5-sided); thecae oblong, 0.3–0.5 mm wide, contiguous or ± parallel to one another; sterile staminate flowers 4–6-sided, 1.1–1.5 mm long, 0.8–1.3 mm wide. INFRUCTESCENCE with berries orange; seeds 3–4 per locule, 1–1.1 mm long, 0.5–0.6 mm diam.

Flowering in *Philodendron lentii* appears to occur during the dry season and early rainy season (February, March, June, and July). Post-anthesis collections exist from January, March through July, and November, indicating a somewhat broader range of flowering. Most post-anthesis inflorescences were collected between March through July. Immature fruits are known from January, April, and July while mature fruits are known from April, June, and July.

Philodendron lentii ranges from Costa Rica (Cartago) to Panama (Chiriquí to Coclé), from (210)670 to 1800 m elevation in *Premontane rain forest* and *Tropical Lower Montane rain forest* life zones. In Costa Rica, this species is apparently rare, having been collected only near Tapantí and Moravia in Cartago Province and near Cariblanco in Alajuela Province. In Panama, it has been collected mostly in the Fortuna Dam region, at Cerro Colorado (both Chiriquí), at Santa Fe in Veraguas and at El Valle and El Copé in Coclé Province.

Philodendron lentii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata.* This species is distinguished by its somewhat scandent habit; elongate internodes; deciduous cataphylls; D-shaped to broadly sulcate petioles (about as long as the blades); ovate, subcordate blades with the few basal veins free; and one to two large inflorescences with the spathe white externally and purplish internally on the tube. Also characteristic are the orange berries. Especially useful for recognition is the upper dried blade surface, which usually dries dark with the lateral primary and minor veins weakly raised.

Philodendron lentii may be confused with *P. heleniae,* which has blades of similar size and shape with few pairs of free basal veins and petioles about as long as the blades. That species differs in having more slender stems, subterete petioles, and several to many small, red inflorescences. Although a few collections of *P. lentii* (*Knapp 4970, Thompson 5022*) report the spathe to be red, these cannot be confused with *P. heleniae,* owing to the much larger size of the spathes (mostly more than 12 cm long vs. mostly less than 10 cm long for *P. heleniae*).

Possibly also belonging to this species is a sterile collection from Ecuador (Esmeraldas), *Croat 72298,* which differs in having internodes to 30 cm long, more numerous primary lateral veins (to ca. 20), and interprimary veins also sunken on live plants giving the blade the appearance of having very close primary lateral veins. This collection also differs in having the cross-veins prominulous on the lower surface toward the margin. Despite these differences, this Ecuadorian collection surely represents either *P. lentii* or another closely related new species.

Philodendron lentii is named in honor of Roy Lent, who first collected the species in 1967. Lent, a resident of Costa Rica, has been an important collector over many years and has collected many new species of Araceae.

Additional specimens examined. COSTA RICA. **Alajuela**: 3 mi. S of Cariblanco, 760 m, *Croat 35777* (MO). **Cartago**: Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36592* (F, MEXU, MO, US); Río Grande de Orosi, 0.5 km W of Tapantí, 1200 m, *Lent 909* (CR, F). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, near Continental Divide, 1170 m, 8°44′N, 82°17′W, *Croat 66647* (B, CAS, CR, K, MO, PMA, US); 1200 m, *60360*

(CAS, MO); 1.2 mi. N of Divide, 910 m, 8°44′N, 82°17′W, *Croat 60441* (K, MO, US). **Chiriquí**: Cerro Colorado, vic. of Cerro Colorado Copper Mine Development, 28 mi. above San Félix, 1200–1500 m, *Croat 33273* (MO); Cerro Pate Macho, ca. 5 mi. NE of Boquete, 1800–2200 m, *Croat 48567A* (MO); 1600–1700 m, 8°48′N, 82°23.5′W, *Grayum et al. 6358* (MO); vic. of Boquete, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66395A* (MO); *66391* (MO); *66355* (CM, MO); Fortuna Dam area, 1100–1200 m, 8°45′N, 82°05′W, *Thompson 5022* (CM, MO); 8 km N of Los Planes de Hornito, 1250–1300 m, 8°45′N, 82°12′W, *Knapp 4970* (MO, NY); 11.8 mi. N of Los Planes de Hornito, 1400 m, *Croat 48682* (CM, MO); 10.8 mi. beyond Los Planes de Hornito, ca. 1400 m, *Croat 48712* (MO); 10.1 mi. NW of Los Planes de Hornito, 1250 m, 8°45′N, 82°17′W, *Croat 50041* (CM, MO); 10 mi. NW of Los Planes de Hornito, 1260 m, *Croat 50102* (MO, NY, PMA); Chiriquí Grande–Fortuna, 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60007* (K, MO, US); *60069* (K, MO, US); Gualaca–Chiriquí Grande, 8 mi. N of Los Planes de Hornito, 1.4 mi. W of Centro de Operaciones, along trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67923* (CM, MO); near Fortuna Lake, 8°45′N, 82°18′W, *Croat & Zhu 76388* (MEXU, MO); N edge of lake, ca. 1100 m, ca. 8°45′N, 82°15′W, *McPherson 9078* (MO, NY); Fortuna Dam, 1200 m, *Hammel 2196* (MO); Quebrada Arena, 1050 m, 8°45′N, 82°16′W, *Hammel et al. 14706* (CR, MO); 26 km past Gualaca, 670 m, 8°35′N, 82°19′W, *Hoover 1329* (CAS, MO). **Coclé**: Penonomé–Coclecito, above Río Cascajal, 5.7 mi. N of Llano Grande, 210 m, 8°40′N, 80°26′W, *Croat 67538* (MO, PMA); El Copé region, Alto Calvario, Continental Divide, 5.2 mi. above El Copé, 930 m, *Croat 49204* (MO); Alto Calvario, 710–800 m, 8°39′N, 80°36′W, *Croat 68724* (MO); El Valle region, *Croat 14367* (MO); 2700 ft., *Sytsma et al. 4369* (CR, MO); ca. 800 m, *Croat 25434* (F, MO); *Gentry & Dwyer 3683* (MO); 900–930 m, *Croat 37481* (F, MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76740* (MO, US); Cerro Gaital, 800–900 m, 8°37′N, 80°07′W, *McPherson 11211* (L, MO); 830–900 m, 8°36′N, 80°07′W, *Croat 74812* (MO, PMA); *Hartman 3962* (OS); 1000–1100 m, 8°37′N, 80°07′W, *McPherson 12150* (MO); N slope of Cerro Gaital, 800 m, 8°38′N, 80°07′W, *Churchill 3924* (F, MO). **Veraguas**: Santa Fe region, Alto de Piedra, 800–950 m, 8°33′N, 81°08′W, *Croat 67004* (MO); Parque Nacional Cerro Tute, Alto Piedra–Calovébora, 0.5 mi. N of Alto Piedra, 800–1030 m, *Croat & Zhu 76897* (MO); 1000–1250 m, *Croat 48931* (MO).

Philodendron ligulatum Schott, Prod. Syst. Aroid. 224. 1860. TYPE: Cultivated from Central America, *Wendland s.n.* (holotype, W? destroyed). Costa Rica. Limón: Ref. Nac. Barra del Colorado, between Río Chirripocito and Río Sardina (Sardinal), 10°38′N, 83°45′W, 12 m, 22 Apr. 1990, *Grayum 9823* (neotype, MO; isoneotype, CR). Figures 269–271.

Hemiepiphytic, usually scandent or appressed-climbing or sometimes epiphytic, sometimes occurring high into canopy, rarely terrestrial; stem appressed-climbing or scandent (flowering stems often loose, semi-erect or spreading), green, sometimes with white, waxy coating; leaf scars conspicuous, 1.5–2 cm long, 1–1.8(3) cm wide; internodes sometimes weakly flattened on one side, (1)3–9(20) cm long, 0.5–3 cm diam., usually longer than broad, medium to dark green or gray-green to brownish, weakly glossy, drying gray-green to pale yellow-brown, sometimes irregularly ridged or cracked, sometimes closely tranverse-fissured; epidermis peeling, bubbling or with loose flakes; roots several per node, 15–45 cm long, drying 1–2 mm diam.; cataphylls usually sharply 2-ribbed, sometimes weakly and bluntly 1–2-ribbed, sometimes sharply D-shaped with adaxial margins winged to 6 mm high, 14–19 cm long, sharply flattened, with obtuse medial rib, green to whitish, sometimes tinged reddish, densely dark-lineate, sometimes densely dark-speckled, deciduous intact, margins minutely undulate; **petioles** (7)20–38 cm long, 5–15 mm diam., subterete to obtusely flattened, rarely D-shaped, sometimes with a thin, medial rib toward apex, sometimes with adaxial margins winged to 6 mm high, spongy but brittle (fresh), medium to dark green, obtusely to sharply flattened to sulcate adaxially, the margins at least sometimes acute, broadly rounded abaxially, surface matte to semiglossy, densely short dark green-lineate or speckled, with a deep maroon to purple ring around apex; sheath flattened, unopened, to 3–10 cm long, for up to half the length of the petiole; **blades** oblong-elliptic to narrowly ovate or narrowly oblanceolate-elliptic, subcoriaceous, weakly to moderately bicolorous, acuminate to long-acuminate at apex (the acumen inrolled or apiculate and sometimes downturned, 1–4 mm long), subcordate, obtuse to narrowly rounded or weakly cordate at base, (14)18–61 cm long, 8–19 cm wide (1.57–5.4 times longer than wide), (1.1–3.89(6.3) times longer than petiole), margins weakly undulate; upper surface dark green, semiglossy to moderately glossy, drying blackish brown to dark grayish or grayish brown, lower surface moderately paler, matte to weakly glossy, mottled violet-purple or maroon, drying dark olive-green to yellow-brown, dark olive-brown or dark brownish black; posterior lobes, when present, rounded to narrowly rounded, about as broad as long, 4–5 cm long, 5.5–6.6 cm wide, held close to petiole; sinus somewhat V-shaped, 0.5–3 cm (mostly 2.5 cm) deep; midrib flat to broadly convex, concolorous to paler than surface, sometimes sparsely purple-speckled near base above, narrowly rounded to convex to broadly convex, sometimes round-raised, paler or darker than surface, or sometimes concolorous below, sometimes sparsely purple-speckled near base below; basal veins not evident or 1–3 per side; primary lateral veins 4–8(12) per

side, departing midrib at a 40–70(75)° angle, ± straight or slightly curved to the margins, dark green, weakly sunken to etched, concolorous above, weakly raised to convex and paler than surface below (sometimes with purple spots on older leaves), drying brownish; interprimary veins obscure to impressed, paler than surface, weakly sunken above, weakly raised, darker than surface below; minor veins weakly visible above, very close, obscurely and weakly raised, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1(2) per axil; peduncle (5)7.5–17.5(28) cm long, 7–10 mm diam., subterete, obtusely angular to 3-sided, pale to medium green; **spathe** 10–19.5 cm long, 1.5–2 cm diam. (to 6.5 cm wide when flattened), ((0.8–1.3)1.4–1.6(1.8) times shorter than peduncle), semiglossy, acuminate at apex, barely or not at all constricted, ribbed on back, margins revolute; spathe blade white or cream, sometimes sparsely red-spotted outside, sometimes tinged purple-violet on outer margin, 7–8.5 cm long, 1.7 cm diam. (opening 7.5–7.8 cm long, 3.2–4 cm wide), whitish inside; resin canals bright orange, appearing throughout lower ¾ of spathe and to near base of tube inside; spathe tube oblong, pale to medium green with pale violet nearest base, sparsely red-spotted outside, 6.5–7 cm long, 1.2–1.5 cm diam., glossy, whitish or pale green, sometimes red to violet-purple (B & K purple 5/10) near base or throughout tube inside; **spadix** ± tapered with slight bend, held ± erect, protruding forward from spathe, rounded at apex, (8.3)11–15.5 cm long; pistillate portion light green, (1.4)3.7–6.5 cm long, 9–13(16) mm diam. at apex, 10–14(17) mm diam. at middle, 9–12(15) mm diam. at base; staminate portion (6.8–7.2)10.5–11.2 cm long; fertile staminate portion (9)11–16 mm diam. at base, (7)11–16 mm diam. at middle, (5)9–11 mm diam. ca. 1 cm from apex, broadest slightly above the middle, as broad as or broader than the pistillate portion, as broad as or slightly narrower than the sterile portion; sterile staminate portion generally broader than pistillate portion, whitish or tinged faintly violet, 1–1.2 cm diam.; pistils 1.2–2.7(3.5) mm long, (0.8)1.1–1.9(2.6) mm diam.; ovary (5)6–8-locular, 0.8–1.8(2.4) mm long, (0.8)1.1–1.9(2.6) mm diam., walls embedded with granular, crystal-like particles; locules (0.8)1.1–1.8(2.4) mm long, (0.1–0.2)0.4–0.7 mm diam., ovule sac 0.5–0.7(1–1.3) mm long, with sub-basal placentation; ovules 1 per locule, contained within translucent, gelatinous envelope, 0.2–0.6 mm long, usually longer than funicle; funicle 0.1–0.2(0.4) mm long, style 1–6 mm long, (0.8–10)14–19(26) mm diam., similar to style type B or type D (rarely to type C); central style dome sometimes present; style apex flat to rounded or sloping; style boss sometimes present; funnel shallow when present; stigma somewhat cupulate, truncate, unlobed to subdiscoid, (0.4)0.9–12 mm diam., 0.1–0.3 mm high, covering center of or entire style apex, inserted on center of style apex or style boss or funnel if present, sessile, papillate, semiglossy; the androecium truncate, margins irregularly 4–6-sided, 1–3 mm long; thecae oblong to ovate, sometimes elliptical, 0.3–0.6 mm wide, ± parallel to one another or contiguous; pollen subspheroidal to oblong or obovoid; sterile staminate flowers usually 4–6-sided, 1.2–2.2 mm long, 1.3–2 mm wide. INFRUCTESCENCE with berries oblong-elliptic, 3 mm long; seeds oblong, light yellow-brown, 1.4 mm long, 0.4 mm diam., narrowly ribbed longitudinally. JUVENILE blades with lower surface sometimes tinged maroon.

Philodendron ligulatum ranges from Nicaragua (Chontales and Zelaya) along the Atlantic slope of Costa Rica and along the Atlantic slope and Continental Divide of Panama to Colombia (Antioquia and Chocó). It occurs in *Tropical wet forest* and *Premontane rain forest* life zones, from sea level to 1200 m elevation (to 600 m in Nicaragua and 650 m in Costa Rica).

Philodendron ligulatum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. This species is characterized by its somewhat scandent to appressed-climbing habit; generally elongate internodes; sharply 2-ribbed to obtusely 1-ribbed cataphylls; more or less spongy, obtusely flattened to somewhat D-shaped petioles clearly demarcated from the blade by a purple ring; usually more or less oblong blades narrowly cordulate at the base (or with the blades ovate and cordate) with usually 1–2 free basal veins; and usually 1–2 inflorescences per axil.

This species comprises three varieties. *Philodendron ligulatum* var. *ligulatum* exists throughout the range of the species, whereas varieties *ovatum* and *heraclioanum* are endemic to Panama. See under those varieties for the differences separating them from variety *ligulatum*. *Philodendron ligulatum* var. *ovatum* is endemic to central Panama in Coclé and Veraguas Provinces, while *P. ligulatum* var. *heraclioanum* is known from far eastern Panama in San Blas and Darién.

Philodendron ligulatum is probably close to *P. correae* from upland Chiriquí in western Panama. The latter species differs in lacking distinct primary lateral veins. It also differs in occurring at generally higher elevations (780–1400 m).

Philodendron ligulatum may also be confused with *P. immixtum*, also a vine but with smaller leaves. See under the latter species for a discussion of the differences. *Philodendron ligulatum* may also be confused with *P. wendlandii*. The latter has similar blades and spongy petioles, but differs in being a true epiphyte with short internodes and petioles sharply flattened adaxially and usually much broader than thick.

The protologue of *P. ligulatum* describes a sterile plant, whereas Schott's color plates (Icones) depict fertile material. None can therefore be used as type material. In addition, Engler's *Araceae No. 180* prepared in 1883 and said to have been collected from the living type plant was not studied by Schott. This species is represented by excellent illustrations of fertile material by Schott, one of which could have served as a neotype, but it was deemed best to select a new fertile specimen for the neotype.

The names *Philodendron ligulatum* and *P. lingulatum* (L.) K. Koch (*P.* subg. *Pteromischum*) have been confused in the past. Pursuant to an unpublished request for a recommendation by the Committee for Spermatophyta, the two names have officially been ruled not confusable, hence not homonymous (see Nicolson, 1994: 280).

KEY TO THE VARIETIES OF *P. LIGULATUM*

1a. Petioles sharply D-shaped with undulate lateral margins adaxially; lower leaf blade surface mottled purple-violet or maroon; ovaries with 2 ovules per locule (lacking an obvious ovule sac); eastern Panama, 0–200 m ..... var. *heraclioanum* Croat

1b. Petioles subterete, at most obtusely somewhat flattened adaxially; lower leaf blade surface not colored; ovaries with 1 ovule per locule, contained within an obvious ovule sac; Nicaragua to Panama.

2a. Leaf blades 1.5–1.7 times longer than wide; peduncles longer than spathe; Panama, 770–1200 m ..... var. *ovatum* Croat

2b. Leaf blades 2–4.5 times longer than wide; peduncles shorter than or about as long as spathe; usually occurring below 800 m (rarely to 1200 m) ..... var. *ligulatum*

Philodendron ligulatum Schott var. **ligulatum**

Internodes sometimes weakly flattened on one side, (1)3–9(2) cm long, 0.5–3 cm diam.; cataphylls usually sharply 2-ribbed, sometimes weakly 2-ribbed; **petioles** 7–38 cm long, 5–15 cm diam., subterete, usually at most obtusely somewhat flattened adaxially, sometimes sulcate, sometimes sharply flattened on one margin adaxially, rarely D-shaped; lower leaf blade surface not colored; blades oblong-elliptic, 24–60 cm long, 8–19 cm wide (2.1–4.4 times longer than wide), (1.1–3.9(5.1) times longer than petiole), upper surface drying dark olive-green to brownish; sinus 0.5–3 cm (mostly 2.5 cm) deep; basal veins not evident or 1–3 per side; primary lateral veins 5–8(9) per side, departing midrib at 60–70° angle. INFLORESCENCES 1 per axil; peduncle 7.5–17(28) cm long; **spathe** 10–19.5 cm long, spathe blade white or cream, sometimes sparsely red-dotted outside, spathe blade whitish or sometimes violet-purple near base of tube or throughout inside; spathe tube pale green thoughout, pale violet nearest base, sometimes sparsely red-violet outside; **spadix** (8.3)11–15.5 cm long; pistillate portion (1.4)3.7–6.5 cm long; ovules 1 per locule, contained within an obvious ovule sac; style similar to style type B or D, central dome sometimes present; stigma somewhat cupulate, truncate, unlobed to subdiscoid.

Flowering in *Philodendron ligulatum* var. *ligulatum* occurs in the early rainy season, between May and August, with a few flowering collections from October through March at the end of the rainy season and early dry season. Post-anthesis inflorescences have been collected from February through August (as well as November). It is possible that this species flowers bimodally, once near the beginning of the rainy season and again near the end of the rainy season or the early dry season. Immature fruits are known from July, August, and December, but mature fruits only from December.

Philodendron ligulatum is typically somewhat scandent in Costa Rica but is often more nearly an appressed hemiepiphyte in Panama. In Costa Rica, the number of inflorescences per axil is never more than two but in some areas of Panama up to three inflorescences per axil may be encountered, and in the Santa Rita Ridge area of Panama, a particularly unusual specimen (*Croat 76954*) has up to five inflorescences per axil. That collection also has proportionately somewhat longer petioles than other collections. This unusual specimen is otherwise identical to other plants of the species, even those from the same region. It is perhaps of hybrid origin.

A few Panamanian specimens of *P. ligulatum* var. *ligulatum* from the vicinity of Santa Fe in Veraguas Province (*Croat 25692, 48906A, 66914*) and in Coclé (*Croat 49195*) differ in drying yellow-green and having somewhat more coarse venation. These are somewhat intermediate with *P. ligulatum* var. *ovatum*.

Croat 33306, from 1200 m elevation on Cerro Colorado in eastern Chiriquí Province, has black-drying blades averaging slightly more than two

times longer than broad, and is also somewhat intermediate with *P. ligulatum* var. *ovatum*.

A collection from the southern slopes of Panamá Province in the basin of the Río Madroño (*Croat & Zhu 77041*) is intermediate between *P. ligulatum* var. *heraclioanum* and variety *ligulatum* in having sharply D-shaped petioles lacking undulate-winged margins.

A noteworthy collection from Antioquia Department in Colombia (*Fonnegra et al. 1957*) perhaps also represents *P. ligulatum* var. *ligulatum*, but differs in having the primary lateral veins drying paler than the surface below rather than darker as is the general case.

Additional specimens examined for P. ligulatum *var.* ligulatum. COSTA RICA. **Alajuela**: 3 mi. N of San Miguel, 380 m, *Croat 35643* (MO); Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36262* (MO); near Río Zapote, 1.8–2.7 km S of Río Canalete, ca. 100 m, *Croat 36360* (MO); Naranjo–Aguas Zarcas, 8.5 km NE of Villa Quesada, ca. 600 m, *Croat 46971* (MO). **Guanacaste**: Parque Nacional Rincón de la Vieja Colecta, 400 m, *Rivera 1136* (CR, MO). **Heredia**: La Zona Protectora, SSE of Magsasay, *Schatz & Grayum 707* (DUKE); Finca La Selva, at confluence of Río Sarapiquí and Río Puerto Viejo, Atlantic slope, 50–80 m, 10°26′N, 84°01′W, *Grayum 7673* (CR, MO); *Folsom 9973* (MO); 100 m, *Grayum 2800* (MO); *Hammel 8827* (MO); *Croat 61220* (MO); between Río Sucio and railroad tracks, SW of Finca Zona Ocho, Río Frío de Sarapiquí, ca. 110 m, 10°18′N, 83°52′30″W, *Grayum & Hammel 5567* (CR, MO); near Porto Viejo along road near Río Sucio, 20 m, *Croat 35730* (MO). **Limón**: Hitoy Cerere reserve, SW of Valle La Estrella, 150–550 m, 9°39′N, 83°02′W, *Grayum et al. 5806* (CAS, CR, MO, PMA, US); Turrialba–Limón, ca. 11 mi. S of Siquirres, 650 m, *Croat 43331* (MO); Refugio Nacional de Vida Silvestre Barra del Colorado, Río Chirripocito–Río Sardina, 12 m, 10°38′N, 83°45′W, *Grayum 9823* (CR, MO). NICARAGUA. **Chontales**: Cerro Las Nubes, El Tamagás–Loma San Gregorio, ca. 2 km N of Santo Domingo, 600 m, *Grijalva & Ríos 3455* (MO). **Matagalpa**: NW of Cerro Musún, 500–800 m, *Araquistain & Moreno 2570* (MO). **Zelaya**: Colonia Kururia, <50 m, ca. 14°41′N, 84°04′W, *Pipoly 3974* (MO); plantel of Neptune Mining Company, NE Bonanza, 200–350 m, ca. 14°01′N, 84°35′W, *Stevens 13029* (MO); Río Iyas, between Quebrada El Toro, 260–280 m, *Vincelli 371* (MO); Río Sucío, 2 km E of Bonanza, 140 m, *Neill 4011* (K, MO). PANAMA. **Bocas del Toro**: Station Milla 7.5 on Changuinola–Almirante Railroad, 100 m, *Croat 38098* (CM, COL, CR, F, MO, NY); Almirante–Ojo del Agua, 3–6 km W of Almirante, 30–200 m, *Croat 38212* (F, K, MO); vic. of Chiriquí Lagoon, *Wedel 1479* (F, GH, MO). **Canal Area**: along Río Indio de Gatún, near sea level, *Pittier 2794* (US). **Chiriquí**: Cerro Colorado, along Continental Divide 20–28 mi. from San Félix, 1200–1500 m, *Croat 33306* (MO). **Coclé**: La Mesa, N of El Valle de Antón, 785 m, 8°37′N, 80°08′W, *Croat 67113* (MO, PMA); 800 m, *25370* (F, MO, US); 800 m, 8°36′N, 80°07′W, *Croat & Zhu 76669* (MO); *76694* (CM, MO, NY, PMA); Alto Calvario, 5.2 mi. above El Copé, 930 m, *Croat 49195* (BR, CM, DUKE, F, GH, HNMN, MO, PMA, TEX, WIS); 750–900 m, *44734* (MO); 2700 ft., *Sytsma et al. 4343* (MO); Quebrada Mollejón, ca. 5 mi. N of El Copé, 700 m, *Croat 75050* (MO); road to Coclesito, 12 mi. from Llano Grande, 200 m, 8°47′N, 80°28′W, *Churchill et al. 4018* (F, MO). **Colón**: Santa Rita Ridge road, ca. 22 km from Transisthmian Highway, 500 m, 9°25′N, 79°40′W, *Hammel et al. 14474* (L, MO); along trail to Río Indio, beginning 10.6 km from highway, 380 m, *Croat 44302* (MO, NY, PMA); 26 km from highway, 500 m, 9°26′N, 79°57′W, *Knapp et al. 1737* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76954* (B, CAS, COL, CR, F, K, MEXU, MO, NY, PMA, SCZ, US, VEN); Sabanitas–Portobelo, Río Piedras Lumber Road, 250 m, 9°22′30″N, 79°41′30″W, 250 m, *Croat 75164* (MO, PMA), *75171* (MO); Portobelo–Nombre de Dios, 4.1 mi. W of Nombre de Dios, 50 m, 9°35′N, 79°33′W, *Croat 67318* (AAU, CAS, CM, COL, CR, DUKE, F, G, HNMN, K, KYO, L, LE, MBM, MO, NY, P, PMA, QCA, RSA, TEX, US, VDB); Portobelo–Nombre de Dios, vic. Río Indio, 50 m, *Croat 33603* (MO, PMA); above road 18 km past Sardinilla on road to Nombre de Dios, 150–300 km, *Croat 26100* (MO); Río Boquerón, past Salamanca, 300–400 m, 9°20′N, 79°35′W, *Knapp & Sytsma 2389* (MO); Río San Augustín flowing into Río Guanche, ca. 0 m, 9°30′N, 79°40′W, *Churchill et al. 6017* (CAS, MO, NY, PMA, RSA); Río Iguanita–Portobello Road, <50 m, 9°27′N, 79°42′W, *Croat 49778* (F, MO); Río Guanche above bridge on Portobelo Road, ca. 3–5 km above bridge, 50–200 m, *Croat 36970* (MO); 4 km up Río Guanche, 0–50 m, 9°30′N, 79°40′W, *Knapp 997* (MO); ca. 1.5 mi. S of road, <100 m, 9°27′N, 79°40′W, *Croat & Zhu 76237* (MO); vic. of Guásimo on Río Miguel de la Borda, *Knapp 9983* (MO, SCZ); Río Fató, 10–100 m, *Pittier 3867* (NY, US). **Panamá**: El Llano–Cartí Road, 6.8 mi. from highway, 350 m, *Croat 49102* (MO); Cerro Jefe, 15.4 mi. from Panamerican Highway, ca. 1000 m, *Croat 49092* (MO); Serranía de Majé, high point of ridges S of Ipetí, 650–800 m, 8°45′N, 77°30′W, *Knapp et al. 4490* (MO); El Valle de Madroño–La Sacna, 2.5 mi. N of El Valle de Madroño, 180 m, 9°14′25″N, 79°05′W, *Croat & Zhu 77041* (MO). **San Blas**: El Llano–Cartí Road, 1–2 mi. N of Nusagandi on road to Cartí, 250–275 m, 9°20′N, 79°W, *Croat & Zhu 76580A* (MO). **Veraguas**: vic. of Santa Fe, past Escuela Agrícola Alto de Piedra, at Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66914* (MO, US); ca. 5–8 km beyond agricultural school, 730–770 m, *Croat 25962* (F, MO); Santa Fe–Calovébora, 1.7 mi. past Alto Piedra School, 1.5 mi. beyond Quebrada Cosilla, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76862* (MO); Río Concepción, *Lewis 2793* (MO, NY).

Philodendron ligulatum var. **heraclioanum** Croat, var. nov. TYPE: Panama. Darién: Parque Nacional Cerro Pirre, vicinity of station along Río Perisenico, 110 m, 8°01′N, 77°44′W, 26 July 1994, *Croat & Zhu 77098* (holotype, MO– 04619347–9; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GB, GH, HUA, IBE, K, L, M, MEXU, NY, OOM, P, PMA, QCA, SEL, TEX, U, US, VEN, WIS). Figures 274–276.

Internodia 1 cm longa, 1.1–2.5 cm diam.; cataphylla 15–20 cm longa, obtuse 2-costata, decidua; petiolus acute D-formatus, (8.5)20–28 cm longus, marginibus alatis; lamina (29)46–61 cm longa, (8.5)12–15 cm lata, oblongo-elliptica vel anguste oblanceolato-elliptica, obtusa basi, in

sicco nigrescens; inflorescentia 1; pedunculus (5)13–15 cm longus, 1 cm diam.; spatha 10–12 cm longa.

Internodes short, to 1 cm long, 1.1–2.5 cm diam., usually longer than broad, medium green, semiglossy, drying pale yellow-brown, conspicuously and irregularly ridged and cracked; roots moderately few, to 30 cm long, 4 mm diam., reddish brown, weakly glossy, finely scaly; cataphylls 15–20 cm long, bluntly 1–2-ribbed, sharply 2-ribbed near apex; **petioles** (8.5)20–28 cm long, sharply D-shaped, with adaxial margins winged (to 6 mm high); **blades** oblong-elliptic to narrowly oblanceolate-elliptic, obtuse to narrowly rounded at base, (29)46–61 cm long, (8.5)12–15 cm wide ((2.9)4.3–5.4 times longer than wide), (2–2.6(6.3) times longer than petiole), upper drying blackish, lower surface matte, heavily tinged or mottled violet-purple or maroon, drying dark brownish black; midrib narrowly rounded and paler than surface below with maroon spots on older veins; basal veins lacking; primary lateral veins 5–12 per side, departing midrib at a 40–50° angle to the margins, green with maroon spots on older plants. INFLORESCENCES 1 per axil; peduncle (5)13–15 cm long, 1 cm diam.; **spathe** pale green, 10–12 cm long, to 6.5 cm wide when flattened, tinged violet-purple on outer margin and at base outside and at base inside; spathe blade greenish inside; spathe tube pale green, glossy inside; **spadix** 9.5–12 cm long; pistillate portion 4.3 cm long in front, 3.6 cm long in back; ovules 2 per locule, contained within transparent matrix, style similar to style type C; style funnel shallow to moderately deep. INFRUCTESCENCE with berries oblong-elliptic, 3 mm long; seeds oblong, light yellow-brown, 1.4 mm long, 0.4 mm diam., narrowly ribbed longitudinally. JUVENILE blades with lower surface heavily tinged maroon.

Flowering in *Philodendron ligulatum* var. *heraclioanum* is poorly known. Pre-anthesis flowering collections were seen from March and in July. The inflorescence on the July collection was nearly fully emerged so that it would certainly have opened in less than one month. Immature fruits were seen in October.

Philodendron ligulatum var. *heraclioanum* is endemic to Panama, known definitely only from the type locality at the base of Cerro Pirre in Darién Province from 50 to 200 m elevation in a *Premontane wet forest* life zone.

This variety is characterized by its bluntly two-ribbed cataphylls; sharply D-shaped, marginally winged petioles; and the oblong-elliptic to narrowly oblanceolate-elliptic, blackish drying blades heavily tinged with maroon on the lower surface when young.

Philodendron ligulatum var. *heraclioanum* differs from both varieties *ligulatum* and *ovatum* in its sharply D-shaped petioles with undulate-winged margins; in having 2 ovules per locule without an obvious ovule sac (vs. 1 ovule per locule contained in an ovule sac for the other two varieties); and in the maroon coloration of the lower surface of the young blades. In contrast, the other two varieties have petioles that are typically terete or subterete, merely obtusely flattened adaxially.

Philodendron ligulatum var. *heraclioanum* may be confused with *P. pseudauriculatum*, but the latter differs in having the petioles unwinged and, at most, obtusely flattened adaxially. In addition, *P. pseudauriculatum* has never been reported to have the blades purplish on the lower surfaces.

A collection from San Blas in far eastern Panama is probably also this variety; it differs in having much longer internodes (to 10 cm long and drying ca. 5 mm diam.) and proportionately shorter petioles.

Philodendron ligulatum var. *heraclioanum* is named in honor of Panamanian collector Heraclio Herrera, who was one of the first to collect the taxon.

Additional specimens examined. PANAMA. **Darién**: Cerro Pirre National Park, W side of Cerro Pirre, base camp, 50 m, 8°N, 77°48′W, *Croat 68963* (MO); Parque Nacional Darién, Estación Rancho Frío, N base of Cerro Pirre, ca. 9 km S of El Real, Quebrada Perisenico, 70–270 m, 8°01′N, 77°44′W, *Hammel et al. 16145* (MO). **San Blas**: Quebrada Masargandí, Isla de Tubuala, 200–400 m, 8°54′N, 77°46′W, *Herrera 1304* (CAS, CM, MO, PMA).

Philodendron ligulatum var. **ovatum** Croat, var. nov. TYPE: Panama. Veraguas: vicinity of Santa Fe, along road between Alto Piedra and Calovébora, 0.5 mi. N of Alto Piedra, on slopes of Cerro Tute, Parque Nacional Cerro Tute, 800–1030 m, 15 July 1994, *Croat & Zhu 76888* (holotype, MO– 4619517; isotypes, B, COL, CR, F, K, NY, PMA, US, VEN). Figure 273.

Internodia 1–6(8) cm longa, 1–1.7(3) cm diam.; cataphylla 13–16 cm longa, incostata vel acute 2-costata; petiolus (10)15–19 cm longus, 7 mm diam.; lamina anguste ovata, subcordata basi, (14)18–26(39) cm longa, (8.5)12.5–16 cm lata, in sicco viridibrunnea supra, flavibrunnea infra; inflorescentia 1; pedunculus 12–16.5 cm longus, 7–10 mm diam.; spatha 11.5–18.5 cm longa, extus omnino viridalba; tubo spathae intus rubro basi.

Internodes 1–6(8) cm long, 1–1.7(3) cm diam., sometimes to 3 m or more long, sometimes covered with a thin layer of translucent white wax; cata-

phylls 13–16 cm long, unribbed to bluntly 1-ribbed or sharply 2-ribbed (ribs to ca. 4 mm high, incurled); **petioles** (10)15–19 cm long, 7 mm diam., subterete and obtusely flattened toward apex; **blades** narrowly ovate, weakly cordate at base, (14)18–26(39) cm long, (8.5)12.5–16 cm wide (1.57–1.65 times longer than wide), upper surface drying greenish brown to blackened, lower surface drying yellowish brown to dark olive-brown; posterior lobes rounded to narrowly rounded, 4–5 cm long, 5.5–6.6 cm wide, narrowly rounded to obtuse; sinus somewhat V-shaped, 2.5–3 cm deep; midrib convex to round-raised below; basal veins 2–3 per side, free to base; primary lateral veins 4–6 per side, departing midrib at a 55–65(75°) angle. INFLORESCENCES 1 per axil; peduncle 12–16.5 cm long, 7–10 mm diam.; **spathe** 11.5–18.5 cm long, 1.5–2 cm diam. (0.8–0.95 times as long as peduncle), greenish white throughout; spathe tube sometimes pale to medium green outside, pale to medium green, sometimes red to purplish violet at base inside; **spadix** 10–12.5 cm long; pistillate portion 4–4.5 cm long; pistils 1.7–1.8 mm long, 1.7–1.8 mm diam., whitish; ovules 1 per locule, contained within transparent, gelatinous ovule sac, style similar to style type B; stigma subdiscoid, unlobed, often truncate.

Flowering in *Philodendron ligulatum* var. *ovatum* occurs in the rainy season. Collections at or near anthesis have been made in July, October, and November. Observations on a single plant in July showed a series of inflorescences with one at anthesis and one other on the same stem in postanthesis condition. No fruiting collections are known.

Philodendron ligulatum var. *ovatum* is endemic to Panama, known only from Santa Fe in Veraguas and at El Copé in Coclé Province in *Premontane rain forest* at 770 to 1200 m elevation.

This taxon is characterized by its smooth, brown-drying stems, elongate internodes, sharply 2-ribbed to bluntly 1-ribbed deciduous cataphylls, subterete to D-shaped petioles about as long as the blades, ovate, subcordate blades with two to three pairs of free basal veins, and solitary inflorescences with the peduncle longer than the spathe.

Philodendron ligulatum var. *ovatum* differs from variety *ligulatum* in having blades 1.5–1.7 times longer than wide (vs. 2–4.5 times longer than wide in var. *ligulatum*); peduncles longer than the spathe (vs. shorter than or about as long as the spathe for var. *ligulatum*); and two ovules (rather than one) per locule. In addition, *P. ligulatum* var. *ovatum* usually occurs at higher elevations (770 to 1200 m) vs. usually below 800 m for *P. ligulatum* var. *ligulatum*. Curiously, leaves of a few specimens of *P. ligulatum* var. *ovatum* dry yellowish green or brown, as opposed to the somewhat blackened color typically associated with the species.

Philodendron ligulatum var. *ovatum* may also be confused with *P. lentii* Croat & Grayum with which it also occurs in the El Copé region. That species differs in having usually more than ten pairs of primary lateral veins with several pairs of interprimary veins visible between them on the dried upper blade surfaces (vs. only about five pairs of primary lateral veins and no interprimaries visible on the upper dried blade surface). In addition, the spathes of *P. lentii* are typically short-pedunculate.

Additional specimens examined. PANAMA. **Coclé**: Alto Calvario, ca. 6 mi. N of El Copé, 770 m, 8°38′N, 80°35′W, *Croat & Zhu 76754* (MO); *Croat 67572* (MO); *68767A* (CM, MO); 1200–1300 m, 8°38′N, 80°36′W, *Sytsma 1903* (MO); 650–850 m, *Folsom 6221* (MO, PMA); ca. 5 mi. N of El Copé, 900–1000 m, *Croat & Zhu 75055* (K, MO, SCZ). **Veraguas**: vic. Escuela Agrícola Alto Piedra near Santa Fe, 1050–1150 m, *Croat 48906A* (MO).

Philodendron llanense Croat, sp. nov. TYPE: Panama. Panamá: vic. of Cerro Jefe, along road to summit which leads S off main road to La Eneida, 750–800 m, 9°14′N, 79°22′W, *Croat 67092* (holotype, MO–3582669–71; isotypes, B, CAS, COL, CR, F, G, HUA, K, M, MEXU, NY, P, PMA, SCZ, SEL, TEX, US, VEN). Figures 268, 277, 278.

Planta plerumque hemiepiphytica, raro terrestris; internodia 5–10 cm longa, 4–6 cm diam.; cataphylla 30–41 cm longa, plerumque incostata, persistentia semi-intacta aut ut fibrae nodis supremis; petiolus subteres, 49–76 cm longus, 1–2 cm diam.; lamina 51–77 cm longa, 39–60.4 cm lata, late ovato-cordata; nerviis lateralibus I (4)5–6(7) utroque; inflorescentia (1)2–3; pedunculus 3–10.5 cm longus; spatha 12.5–24 cm longa, lamina spathae extus atriviridi, intus alba; tubo spathae atrirubroviolaceo basi; pistilla (5)6–8(9)-locularia; loculi (6)12(20)-ovulati.

Usually hemiepiphytic, rarely terrestrial; stem appressed-climbing, to 1 m long, sap clear, viscous, sticky, spicy- to turpentine-like-scented; internodes usually short, dark green, soon gray-green, finally light brown, moderately scurfy, semiglossy, 5–10 cm long, 4–6 cm diam., usually broader than long, sometimes longer than broad; roots greenish, becoming brown, 3–4 mm diam.; cataphylls 30–41 cm long, usually unribbed, sometimes weakly 2-ribbed, light to medium green, sharply and broadly D-shaped, persisting semi-intact or as fibers at uppermost nodes, fibrous below, the fibers thin, pale, disorganized, light gray. LEAVES erect-spreading, clustered at or near stem apex; **petioles** 49–76 cm

long, 1–2 cm diam., subterete, somewhat spongy, pale to medium green, rarely with medial rib adaxially, with adaxial margins sometimes acute, surface semiglossy to almost matte, densely and in conspicuously short-lineate, at least sometimes with a dark green ring at apex; **blades** broadly ovate-cordate, moderately coriaceous, abruptly acuminate, sometimes acute at apex, conspicuously cordate at base, 51–77 cm long, 39–60.4 cm wide (1.2–1.6 times longer than wide), (0.9–1.2 times longer than petiole), about equal in length to petiole, margins ± hyaline, upper surface dark green, semiglossy to moderately glossy, drying dark brown, lower surface semiglossy to almost matte, paler, drying yellow-brown; anterior lobe 41–60 cm long, 39–60.4 cm wide (0.9–1.4 times longer than wide), (2.2–3 times longer than posterior lobes); posterior lobes 18.5–24 cm long, 16–31 cm wide, obtuse; midrib almost flat to broadly convex to broadly flattened, paler than surface above, convex, paler than surface below; basal veins 4–6 per side, with 0–1 free to base, the remaining coalesced 6–9 cm; posterior rib usually naked for 2–3 cm; primary lateral veins (4)5–6(7) per side, flat to weakly sunken, paler than surface above, convex, paler than surface below; minor veins moderately obscure above, darker than surface, arising from both the midrib and primary lateral veins, drying prominulous above and below; secretory canals distinct. INFLORESCENCES (1)2–3 per axil; peduncle 3–10.5 cm long, 1.1–1.2 cm diam., coarsely white striate near apex; **spathe** 12.5–24 cm long (1.7–5 times longer than peduncle), oblong, dark to medium green throughout outside, markedly white-lineate near the base, faintly so above the base, moderately constricted above the tube; spathe blade weakly and densely lineate outside (opening broadly elliptic in face view), white inside; spathe tube cylindrical, markedly white-lineate near the base outside, 6–8.5 cm long, 3–5.5 cm diam., dark reddish violet, suffused onto base of blade inside; **spadix** sessile, greenish white throughout, ± cylindrical, protruding prominently forward from and out of the end of spathe (at anthesis), 10–17 cm long; pistillate portion creamy white (anthesis), reddish (pre-anthesis), weakly tapered toward apex, 4.1–5 cm long, 2.5–5 cm long in front, 1 cm diam. throughout, 1.1–1.5 cm diam. at apex, 1.4–1.6 cm diam. at middle, 1–1.5 cm wide at base; staminate portion 6–14.4 cm long; fertile staminate portion white, ± cylindrical 1.1–1.7 cm diam. at base, 1.1–1.9 cm diam. at middle, 7–10 mm diam. ca. 1 cm from apex, broadest ± at the middle, slightly broader than the pistillate portion, narrower than the sterile portion; sterile staminate portion 1.1–1.9 mm diam.; pistils 1.2–4.8(7.2) mm long, 1.1–2.4(4.3) mm diam.; ovary (5)6–8(9)-locular, 1.5–3.5(6.8) mm long, 1.1–2.4(4.3) mm diam., walls sometimes embedded with granular, crystal-like particles, locules 1.5–3.5(6.8) mm long, (0.2)0.6–1.5 mm diam., thin and membranous, ovule sac 1.9–2 mm long, with axile placentation; ovules (6)12(20) per locule, 1–2-seriate, contained within gelatinous ovule sac, 0.2–0.45 mm long, slightly longer than funicle; funicle 0.1–0.3 mm long, style 0.3–0.7 mm long, 1.3–1.6(2.5, 4.5) mm diam., similar to style type B; style crown truncate at apex with lobed depression; style apex rounded; stigma button-like, unlobed or weakly lobed, truncate, 1.1–2.2 mm diam., 0.5–1.0 mm high, covering entire style apex, sometimes depressed medially; the androecium truncate, margins irregularly 4–6-sided; thecae oblong to cylindrical, 0.4 mm wide, ± parallel to one another, ± contiguous; sterile staminate flowers acutely to bluntly 4–6-sided, 2.1–2.4 mm long, 1.1–2 mm wide. INFRUCTESCENCE with spathe green outside, orange-brown inside; berries white, 7.2–10 mm long, 3.6 mm diam.; seeds more than 10 per locule, pale yellow. JUVENILE plants terrestrial or epiphytic; internodes short, brown, weakly glossy; petioles 29.2 cm long, ± terete, moderately spongy; blades 28.6–37.7 cm long, 17–28 cm wide; midrib broadly convex above; minor veins distinct below.

Flowering in *Philodendron llanense* occurs at the beginning of the rainy season, in July. Post-anthesis collections exist from January through August, with immature fruits and mature fruits found only in the dry season and early rainy season, mostly January and March but also in June.

Philodendron llanense is endemic to Panama (though to be expected in adjacent Colombia), ranging from 250 to 800 (mostly below 500) m elevation in *Tropical wet forest* and *Premontane rain forest* life zones. This species appears restricted to the region of the Cerro Jefe and the El Llano–Cartí Road (hence the name "llanense").

Philodendron llanense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is characterized by its short, thick internodes; mostly unribbed, semi-intact, or fibrous cataphylls; obtusely flattened to D-shaped petioles (about as long as the blades); thick, broadly ovate-cordate blades with a deeply spathulate to closed sinus and with prominently raised minor veins upon drying; and two to three green inflorescences with the spathe tube dark reddish violet inside.

Philodendron llanense is perhaps most easily confused with *P. schottianum,* which occurs at

mostly higher elevations (generally 1000 to 1600 m) in Costa Rica, rarely to as low as 490 m or as high as 2200 m elevation. It differs from *P. llanense* in having sharply two-ribbed cataphylls persisting more intact and with a prominent yellow epidermis, and blades usually drying with the lower surface more yellowish with the secretory ducts more outstanding and usually with partial "cross-veins" between the minor veins. In addition, *P. schottianum* also has blades proportionately somewhat longer (averaging 1.65 times longer than broad vs. 1.4 times longer than broad for *P. llanense*) and spathes shorter and nearly elliptic with almost no constriction (vs. oblong and noticeably constricted above the tube for *P. llanense*).

Philodendron llanense looks superficially much like *P. ferrugineum* in live condition, and since they occur together, they can be confused. However, *P. ferrugineum* differs in having promptly deciduous cataphylls and somewhat more elongate blades, which dry conspicuously reddish brown.

A single sterile collection (*Croat & Grayum 60209*) from the Atlantic slope near the Continental Divide at 590 m elevation in Bocas del Toro Province may also belong to this species. In addition to being out of range, this collection has the major veins much darker than the surface below.

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna–Chiriquí Grande, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60209* (MO). **Panamá**: El Llano–Cartí Road, 10–12 km from El Llano, 400 m, *Maas & Dressler 1709* (U); Km 9.5 of Pan-American Highway, 200–300 m, 9°15′N, 79°W, *McPherson 10822* (B, MO); Km 12, 350 m, *Mori et al. 4628* (MO); Mile 7, 460 m, 9°19′N, 79°59′W, *Croat 75104* (CAS, MEXU, MO, NY); Km 8–12, ca. 400–450 m, *Nee et al. 8775* (MO, NY, SCZ); Mile 5–9, 200–250 m, 9°15–16′N, 78°59′W, *Thompson 4621* (CM); ca. Km 16–18, 400 m, *Tyson & Nee 7361* (MO, PMA, US); Mile 10.1, 325–350 m, *Croat 67367* (DUKE, K, M, MEXU, MO, NY, US); Mile 12, 200–500 m, *Croat 22910* (MO, PMA); Km 7–12, 360–400 m, *Croat 25118* (MO), *25172* (MO); Mile 10, 330 m, *Croat 33774* (MO), *33819* (MO); Mile 6.8, 350 m, *Croat 49127* (MO); Km 12, *Croat 26031* (MO); Cerro Jefe, near summit, <2900 ft., *Gentry et al. 3501* (MO, NY); 12 km E of Lago Azul, 800–1000 m, *Gentry & Mori 13450* (MO). **San Blas**: El Llano-Cartí Road, 300–500 m, *Liesner 1317* (F, MO, NY, US); Mile 14, 300 m, 9°15′N, 79°W, *Croat 69251* (F, MO); Mile 7, 550 m, 9°43′N, 78°68′W, *60505* (CM, MO, PMA); Km 22, 350 m, 9°19′N, 78°55′W, *de Nevers & Herrera 7859* (MO, PMA); Nusagandi, Sendero Wedar, 300–400 m, 9°18′N, 78°58′W, *McDonagh et al. 216* (BM, MO); 1–2 mi. N of Nusagandi on road to Cartí, 250–275 m, 9°20′N, 79°W, *Croat & Zhu 76577A* (CM, MO); Mile 10.1, 300 m, 9°20′N, 79°W, *76541* (MO, SEL); 1.9 mi. N of Nusagandi, 310 m, *76993* (AAU, CR, GB, MO, NY).

Philodendron madronense Croat, sp. nov. TYPE: Panama. Panamá: Valle de Madroño, ca. 10 road mi. N of La Margarita (near Chepo), just S of Continental Divide along main trail to Cangandí, 350–500 m, 9°19′N, 79°08′W, 21 Feb. 1986, *Hammel & McPherson 14526* (holotype, MO–3490432; isotypes, CM, M, PMA). Figures 279, 280.

Planta hemiepiphytica; internodia usque 2.5 cm diam., longiora quam lata; cataphylla decidua; petiolus subteres, usque 68 cm longus, 1.5 cm diam., aliquantum spongiosus; lamina trisectus, 39.5 cm longis, 15 cm latis; segmentis medianis ellipticis; segmentis lateralibus valde inequilateris, 32–32.8 cm longis, 12.7–13 cm latis; infructescentia 1. Inflorescentia 1; pedunculus usque 22 cm longus, 1 cm diam., in sicco denigratus; spatha usque 20 cm longa, ca. 4 cm diam.; spadix pistillata 11.8 cm longa, ca. 3 cm diam.; spadix staminata ca. 7.5 cm longa, ca. 1 cm diam.; 1 semen in quoque loculo.

Hemiepiphytic vine; internodes to 2.5 cm diam., longer than broad, epidermis drying light brown and semiglossy but conspicuously and irregularly folded; roots several per node, drying dark brown; cataphylls deciduous; **petioles** to 68 cm long, 1.5 cm diam., subterete, somewhat spongy, drying blackened, surface closely and finely ridged; sheathing to 8.5 cm long; **blades** trisect, subcoriaceous, moderately bicolorous, drying weakly glossy, upper surface dark green, drying dark brown, semiglossy, lower surface drying yellow-green, matte; median segments elliptic, somewhat inequilateral, 39.5 cm long, 15 cm wide (ca. 2.5 times longer than wide), (1.5 times longer than lateral lobes), somewhat acuminate at apex, base attenuate and somewhat inequilateral with leafy tissue extending to base on one side, ending 2.5 cm above the base of the other side; lateral segments markedly inequilateral, 32–32.8 cm long, 12.7–13 cm wide, acuminate; the outermost lobes with the inner margins attenuate, tissue ending 1–2.5 cm from base of petioles; outer margins rounded, barely or not at all naked along the sinus; midrib weakly raised, concolorous above, ± round-raised, drying blackened and irregularly ridged below; basal veins lacking; primary lateral veins ca. 25 per side, ca. 4–5 mm apart, departing midrib at a 65–70° angle toward apex, 85–100° angle toward base, gradually curved to the margins, weakly sunken, scarcely more conspicuous than interprimaries above, prominently raised below; interprimary veins numerous, 1–3 between each pair of primary lateral veins; minor veins in part undulate upon drying, close, moderately visible, arising from both the midrib and primary lateral veins. INFLORESCENCES (postanthesis) 1 per axil; peduncle to 22 cm long, 1 cm diam., drying blackened, somewhat spongy; **spathe**

to 20 cm long, ca. 4 cm diam., semiglossy, green outside, red at base inside, drying blackened; pistillate spadix 11.8 cm long, ca. 3 cm diam.; staminate spadix 7.5 cm long, ca. 1 cm diam., moderately tapered to a bluntly acute apex; pistils ± cylindrical, 3–4 mm long, 2.5 mm diam.; ovary 6–7-locular, with sub-basal placentation; locules 2.3 mm long, 0.5 mm diam.; ovules 1 per locule, contained within a transparent evelope; funicle ca. 0.4 mm long (can be pulled free to base), style similar to style type D; style apex flat; style boss pronounced but narrow; seeds 1 per locule, 1.4 mm long.

Flowering in *Philodendron madronense* apparently occurs in the rainy season, since immature fruits have been collected in January.

Philodendron madronense is endemic to central Panama along the border of Panamá and San Blas at 350 to 450 m elevation in a *Tropical wet forest* life zone.

Philodendron madronense is a member of *P.* sect. *Tritomophyllum.* This species is recognized by its scandent habit; elongate internodes; subterete, more or less spongy petioles; and especially by its trisect leaf blades with the medial segments elliptic, inequilaterally attenuate at the base, and with many close prominent primary lateral veins only 4–5 mm apart and departing the midrib at about a 90° angle.

Philodendron madronense is superficially most similar to *P. cotobrusense,* which has deeply 3-lobed blades with more or less elliptic, closely veined divisions. The latter species differs in having the lobes united and confluent at the base and up to five inflorescences per axil. It is also similar to some broad-leaved forms of *P. tripartitum* (e.g., *Whitefoord & Eddy 223*), which occur in eastern Panama, but those differ in having no more than 12 pairs of primary lateral veins, which depart the midrib at a 50–60° angle.

Philodendron malesevichiae Croat, sp. nov. TYPE: Panama. Coclé: vicinity El Valle de Antón, La Mesa, 4 mi. E of El Valle at base of Cerro Gaital, along trail which goes to the S edge and leading to the summit, 830–900 m, 8°36′N, 80°07′W, 25 Mar. 1993, *Croat 74818* (holotype, MO–4342656–57; isotypes, B, COL, CR, F, K, MEXU, NY, PMA, QCNE, US, VEN). Figures 3, 21, 25, 27, 28, 281–284.

Planta terrestris; caulis repens; internodia 2–4 cm longa, 1.5–5 cm diam.; cataphylla 21–29 cm longa, leniter 1–2-costata, in sicco rubrobrunnea, persistentia semi-intacta; petiolus teres, 50–56 cm longus, 8–19 mm diam., anguste sulcatus, sparsim squamus in triente superiore; lamina ovato-cordata, 33–65 cm longa, 23–36 cm lata, in sicco atribrunnea supra, flavibrunnea infra, nervis basalibus 6–9 paribus, superioribus 2–3 liberis ad aliquot basim; reliquiarum coalitis 2–4.5 cm; inflorescentia 1–3; pedunculus 4.5–8 cm longus; spatha 8–20 cm longa; pistilla 5–6-locularia; loculi ca. 19–25-ovulati.

Terrestrial, usually less than 1 m tall, sometimes to 1.5 m, reclining against trees; stem creeping over the ground but well rooted in the soil; internodes 2–4 cm long, 1.5–5 cm diam., pale green to whitish, moderately glossy, usually totally hidden by cataphylls, coarsely but faintly white-short-lineate at apex, drying pale brown, epidermis closely and mostly bluntly ridged with ridges close and cracked transversely; roots moderately few per node, drying 2–3 mm diam., dark brown, closely ridged and weakly scaly; cataphylls 21–29 cm long, unribbed, weakly 1-ribbed or weakly 2-ribbed, whitish to maroon or russet, heavily tinged pink toward lower half, drying dark brown to reddish brown, persisting semi-intact at least toward apex with an underlying network of pale, anastomosing fibers, the outer surface becoming fibrous toward the base. LEAVES erect to erect-spreading; **petioles** 50–56 cm long, 8–19 mm diam., terete or subterete, dark green, tinged purple-violet, weakly glossy, drying dark brown, weakly, obtusely and narrowly sulcate to obtusely flattened adaxially, weakly flattened and often tinged purplish toward apex, faintly striate on surface, sparsely scaly in upper one-third to one-half, scales fine, ± terete, 1–2 mm long, 0.1 mm diam., green; **blades** ovate-cordate, subcoriaceous, moderately bicolorous, acuminate to long-acuminate at apex, prominently cordate at base, 33–65 cm long, 23–36 cm wide, upper surface subvelvety-matte, dark green, drying dark brown, lower surface semiglossy, moderately paler, drying medium yellow-brown; anterior lobe 23–48 cm long, 23–36 cm wide; posterior lobes narrowly rounded, 8–25 cm long, 12–14 cm wide; sinus hippocrepiform, 8–14 cm deep; midrib concave, concolorous or paler above, convex or thicker than broad, much darker olive-green and matte, sometimes tinged maroon near base below, drying darker than surface; basal veins 6–9 per side, with upper 2–3 free to base, part of the remainder coalesced 2–4.5 cm; posterior rib naked for 0.5–3 cm, moderately straight; primary lateral veins (3)5–10 per side, 1.7–2.2 cm apart, departing midrib at a 45–60° angle, downturned acutely at the midrib, weakly sunken to weaky quilted above, convex and darker below, often branching toward the margins, drying blackened; interprimary veins persistent in lower half of blades; minor veins moderately visible but not dis-

tinct when fresh, moderately distinct on drying, weakly undulate, arising from both the midrib and primary lateral veins. INFLORESCENCES 1–3 per axil; peduncle 4.5–8 cm long, to 4 mm diam., pinkish red, coarsely white-lineate toward apex, drying blackened; **spathe** 8–20 cm long, 1–2 cm diam. when furled, to 5.5 cm wide when open (7–11 cm wide when fully flattened), ((2.5)3–3.7 times longer than peduncles), acuminate at apex (acumen 2.5 cm long), semiglossy, in Central America pale yellow-green, darker green toward middle, white along margins, sometimes tinged with pink, the open margin sometimes violet-purple outside, greenish white and matte throughout within, in South America spathe tube sometimes reddish outside, dark red to red-violet, suffused onto lower one-half of blade inside; spathe blade to 15 cm long, white within; spathe tube 7.5–8.5 cm long, to 4.3 cm diam. at anthesis; **spadix** weakly stipitate; 14–15.5 cm long; pistillate spadix (3.4)4–4.3 cm long in front, 2.8–4 cm long in back, 11–16 mm diam. at apex, 1.2–1.8 cm diam. at middle and base; staminate portion 10–13 cm long, 1.2–1.5 cm diam. at base, 1.5–1.8 mm diam. midway, 8–12 mm diam. 1 cm from apex, constricted to 1.5 cm diam. above the sterile portion; sterile staminate portion to 3.4 cm long, 20 cm diam. at base, 10–18 mm diam. at apex; pistils 1.1–2.4(3.5) mm long, 1.2–5 mm diam.; ovary 5–6-locular, with axile placentation; locules 1.3–1.6 mm long; ovules 19–25 per locule, 2–3-seriate, ca. (0.1)0.25–0.3 mm long; funicle as long as or shorter than ovules, ⅓–⅗ as long as the ovule; stigma 1–1.5 mm diam., depressed medially; style similar to style type B, 1 mm diam.; style apex flat to weakly concave; stylar canals arising at base of apical depressions; stigma discoid, 0.8 mm thick, 1.5–18. mm diam.; the androecium truncate to ± prismatic, margins irregularly 4–6-sided, many 6-sided, ca. 0.6 mm long; thecae oblong, ± parallel to one another; sterile staminate flowers clavate, irregularly 4–5-sided to ovoid, 0.9–1.3 mm long.

Flowering phenology in *Philodendron malesevichiae* in Panama is uncertain. All flowering collections are from South America. Flowering collections have been made in February and March and postanthesis collections in March, July, and December. Cultivated collections from Panama grown at the Missouri Botanical Garden flowered in May, June, July, November, and December.

Philodendron malesevichiae ranges from Panama to Colombia. In Panama it is only known from the type locality in *Tropical wet forest* at 830 to 860 m in Coclé Province. In Colombia it has been collected only along the Pacific Coast in Chocó and Valle at 50 to 150 m elevation.

Philodendron malesevichiae is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is characterized by its terrestrial, creeping habit; short internodes; weakly 1–2-ribbed cataphylls drying reddish brown and persisting semi-intact; subterete, narrowly sulcate petioles, which are conspicuously scaly in the upper one-third; and ovate-cordate brown-drying blades with up to eight basal veins, largely coalesced and naked along the hippocrepiform sinus.

This species is most easily confused with *P. glanduliferum.* The latter species differs in having fewer primary lateral veins (2–4 vs. 6–10 for *P. malesevichiae*); posterior ribs that are not at all naked; and a narrow closed or spathulate sinus (vs. hippocrepiform in *P. malesevichiae*).

In Panama there are three other species that have petiolar glands of some form and thus might be confused with *P. malesevichiae.* These are: *P. hammelii, P. verrucosum,* and *P. squamipetiolatum. Philodendron hammelii* differs in its smaller, green-drying blades and petiolar scales mostly less than three times longer than broad. *Philodendron verrucosum* differs in its mostly appressed-climbing habit; scaly cataphylls, inflorescences, and even parts of the lower blade surface; and velvety and matte (rather than semiglossy) upper blade surface. *Philodendron squamipetiolatum* differs in its appressed-climbing habit, long internodes, deciduous cataphylls, green-drying blades, and scaly inflorescences.

Zarucchi & Escheverry 4776, from 2000 m elevation in Antioquia Department, Colombia, may also belong to this species. It is described as having a deep wine-red (rather than green) spathe.

This species is named in honor of Petra S. Malesevich, who has loyally worked with me on all aspects of the *Philodendron* revision. This species is in cultivation at the Missouri Botanical Garden and is deemed a beautiful addition to horticulture.

Additional specimens examined. PANAMA. **Coclé**: La Mesa, above El Valle de Antón, 860–900 m, *Croat 37319* (MO); base of Cerro Gatital, 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76707* (CAS, MO, PMA).

COLOMBIA. **Chocó**: hills above junction of Río Capá and Río Mumbú, up river from Lloró, 80–120 m. 5°37′N, 76°25′W, *Juncosa 1448* (MO). **Valle**: Buenaventura, Bajo Calima region, Buenaventura–Málaga, Km 65–66, 40–65 m, 4°10′N, 77°12′W, *Croat 71057* (COL, MO); 100 m, 4°4′N, 77°09′W, *70162* (CAS, COL, L, MEXU, MO, NY, PMA); Km 49, 150 m, 4°02′N, 77°04′W, *Croat & Bay 75810* (B, CM, COL, F, GB, M, MEXU, MO, PMA, US); Buenaventura–Río Calima, 33.3 km beyond main Cali–Buenaventura Highway, 50 m, 4°02′N, 77°07′W, *Croat 61377* (AAU, COL, MO, PMA, TEX, US); near Km 14

marker, <50 m, 3°56′N, 76°59′W, *Croat 57547* (CM, COL, G, JAUM, MO).

Philodendron mexicanum Engl., in Mart., Fl. Bras. 3(2): 143. 1878. TYPE: Mexico. Veracruz: vic. of Córdoba, *Bourgeau 2176* (holotype, P; isotype, G). Figures 285–288.

Philodendron latisagittium Matuda, Anales Inst. Biol. Univ. Nac. México 22: 371, Fig. 2. 1951. TYPE: Mexico. Chiapas: Mpio. Siltepec, Cascada, mixed humid forest, over humid rocks, 1200 m, 4 Mar. 1951, *Nakamura 31* (holotype, MEXU).

Usually hemiepiphytic, sometimes terrestrial or epilithic; stem scandent, leaf scars conspicuous, 1–1.5 cm long, 1.3–1.6 cm wide; internodes scurfy, glaucous to semiglossy, 18–21 cm long, 1–2 cm diam., longer than broad, medium green to gray-green, epidermis blistering, fissured ± transversely; roots branched at tips, sometimes with swollen nodes along length; cataphylls fleshy, 10–23 cm long, unribbed or bluntly 1-ribbed, pale green, glossy, drying yellowish tan to yellowish green, deciduous intact; **petioles** 22–66.5 cm long, 2–13 mm diam., terete, moderately spongy, medium green, somewhat flattened adaxially, surface semiglossy; **blades** narrowly triangular-sagittate to triangular-hastate, subcoriaceous, acuminate to long-acuminate at apex, sagittate to hastate at base, 23–46 cm long, 14–38 cm wide (1.3–2.7 times longer than wide), (0.6–1.5 times longer than petiole), about equal in length to petiole, margins weakly undulate, upper surface dark green, drying dark brownish green, semiglossy, lower surface drying yellowish green, weakly glossy, paler; medial lobe 19–38 cm long, 8–20 cm wide (1.7–2.7 times longer than posterior lobes), usually 3–3.5 times longer than wide (rarely to 1.7 times longer than wide); posterior lobes 7–19.5 cm long, 4–12.6 cm wide, directed somewhat toward the base, rounded to rarely rounded; sinus parabolic to hippocrepiform or spathulate; midrib broadly sunken, concolorous above, convex, sparsely orange-spotted, slightly paler than surface below; basal veins 0–1(2–5) per side, with 0–1(2–5) free to base, or 1 coalesced, the third and fourth coalesced 3.6–4(13) cm; posterior rib not naked or naked for 0.5–2 cm, directed straight toward the tip of the blade and remaining 1.5–3.5 cm distant from blade margin; primary lateral veins (2)4–5(6) per side, departing midrib at a 55–65° angle, ± straight to the margins, weakly sunken above, raised below; minor veins moderately distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 4–15 cm long, 4–12 mm diam.; **spathe** glossy, 8–16.5 cm long, 1.9–2.3 cm diam. (0.8–1.4(1.5–2.4) times longer than peduncle), acute at apex, the margins paler to clear within; spathe blade greenish to whitish outside; resin canals pale range and appearing as continuous lines inside; spathe tube greenish, sometimes pale reddish tinged outside; red-violet to maroon (B & K red-purple 5/7.5) inside; **spadix** sessile; bluntly rounded to somewhat acute at apex, 10.5–14.7 cm long, broadest toward the apex, constricted below the middle of fertile staminate portion; pistillate portion pale green to green to pale yellow, cylindrical to obovoid, 2–6 cm long, 1 cm diam. at apex, 1.1 cm diam. at middle, 1.3 cm wide at base; staminate portion (6.4)10.3–12.7 cm long; fertile staminate portion creamy white, ± cylindrical, 6–17 mm diam. at base, 7–15 mm diam. at middle, 1.1 cm diam. ca. 1 cm from apex, about as broad as the pistillate and the sterile portions; sterile staminate portion usually broader than the pistillate portion, white to light gray, 1–1.2 cm diam.; pistils 1.6–2(3.5) mm long, 1.1–1.3(2.6) mm diam., transparent white; ovary 5–7-locular, 0.9–2.7 mm long, 1.2–1.4(2.3–2.6) mm diam., with sub-basal placentation; locules 0.9–1.1(2.5) mm long, 0.2–0.4(0.6–0.7) mm diam.; ovule sac 0.6–0.7 mm long; ovules 1–2(3) per locule, digitate, contained within transparent ovule sac, 0.3–0.6(1.1) mm long, longer than funicle; funicle 0.3 mm long, style 0.7(1) mm long, 1.2–1.5(2.4) mm diam., similar to style type B; style apex domed; stigma discoid, at least sometimes lobed both laterally and vertically, sometimes ± cylindrical, 0.7–1.0 mm diam., 0.1–0.3 mm high, covering center of style apex, at least sometimes drying with radial arms sunken between the central peak and the peaks on the end of the arms (*Croat & Hannon 64520*); the androecium truncate, margins irregularly 4–6-sided; thecae ± cylindrical, 0.3–0.4 mm wide, ± parallel to one another; sterile staminate flowers bluntly or acutely 4–6-sided, 1.3–1.9 mm long, 1.3–1.8 mm wide. INFRUCTESCENCE with seeds 1 per locule, yellowish orange, 1.5–1.9 mm long, 0.6–0.8 mm diam.

Flowering in *Philodendron mexicanum* occurs in the mid-dry season and early rainy season (February through May), with post-anthesis collections known February through June (except May) and also in November. Mature fruits are not known. A cultivated collection at Missouri Botanical Garden (*Croat 59933*) flowered perhaps twice per year, in March and in October.

Philodendron mexicanum ranges from Mexico to Colombia, from near sea level to 1900 m elevation, ranging from dry habitats in west-central Mexico (both "Selva Baja Caducifolia" and "Bosque Pino-

Encino") to more humid sites on the Atlantic slope in Vera Cruz to as far south as Honduras in *Tropical moist forest* and to Costa Rica in *Premontane wet forest*. Though widespread, this species is apparently rare and has been collected from relatively few localities, often restricted to mesic enclaves in otherwise arid regions as in the state of Morelos, Mexico. It is one of the most ecologically versatile species in the genus.

Philodendron mexicanum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is recognized by its scandent habit; internodes longer than broad; unribbed, deciduous cataphylls; moderately spongy, somewhat flattened petioles (about as long as the blades); and especially by its narrowly triangular-sagittate to triangular-hastate blades, which dry dark brownish green above and yellowish green below. Sterile collections from Los Ríos and Guayas Provinces of Ecuador (*Dodson & Valverde 6959*) at Jauneche and in Guayaquil Cantón (*Rubio et al. 2008*) may also represent this species. Dodson et al. (1985) erroneously reported the former collection as *P. barrosoanum* G. S. Bunting, a species restricted to the eastern side of the Andes.

Philodendron mexicanum is most similar to *P. angustilobum*, a species ranging from Honduras to Panama. The latter species differs in having leaves that dry more blackened (rather than green to yellow-green as in *P. mexicanum*), and which are more decidedly three-lobed with the medial lobe proportionately narrower and broadest at the middle or even above the middle.

Although the type specimen of *P. mexicanum* was collected in Mexico near Córdoba, most Mexican collections are from the Pacific slope. These have somewhat less prominently narrowed posterior lobes than the type. *Moore & Bunting 8873*, from near the type locality, has the posterior lobes even more conspicuously narrowed than those of the type specimen. In this regard, its blades approach those of *P. angustilobum* in overall shape, but differ in drying greenish to yellowish brown rather than blackened.

A collection from Olancho Department, Honduras (*Croat & Hannon 64520*), is unusual in having a style that dries with radiating arms from a central peak.

The sole Costa Rican collection (*Grayum 5418*) is unusual in having prominently hastate blades. This collection has only a juvenile inflorescence. Further collections may prove it represents a distinct species.

Additional specimens examined. COSTA RICA. **Puntarenas**: Río Guacimal downstream from Monteverde, Cordillera de Tilarán, 1300 m, 10°18′N, 84°49′W, *Grayum 5418* (MO). GUATEMALA. **Quezaltenango**: Finca Pireneos–Patzulín, 1200–1400 m, *Standley 86917* (F); *87007* (F); *87022* (F). **San Marcos**: Volcán Tajumulco, 1300–1500 m, *Steyermark 37968* (F). HONDURAS. **Atlántida**: Quebrada Grande, ca. 10 km SW of La Ceiba, 80–180 m, 15°42′N, 86°51′W, *Liesner 26138* (MO). **Olancho**: San Esteban–Bonito Oriental, Río Grande, 350–400 m, 15°31′N, 85°42′W, *Croat & Hannon 64520* (B, CAS, CM, CR, HNMN, K, L, MEXU, MO, NY, USCG). **Yoro**: Puente Grande, Río Puente Grande (tributary of the Río Agua), *Blackmore & Chorley 4077* (BM, MO). MEXICO. Cultivated at Cornell University, Ithaca, New York, *Moore 7437* (BH); Ixtapan de La Sal, 1900 m, 18°50′N, 99°41′W, *Matuda et al. 32130* (MEXU). **Guerrero**: Atoyac region, above Fila de Caballo, El Paraíso in Parque Nacional de Guerrero, *Croat 67442* (MO). **Morelos**: Cuernavaca, *Bourgeau 1420* (K, P); 1350 m, *Quarles van Ufford 95* (U); 5000 ft., *Pringle 8093* (BH, BM, BR, CM, F, G, GH, H, HBG, ISC, K, LL, MASS, MEXU, MO, NY, P, POM, RSA, UC, US); *Rose & Hough 4439* (US); Río Pollo, below Salto San Antonio, Fraccionamiento San Antonio, W of Colonia Carolina, NW of Center of Cuernavaca, 1500 m, 18°57′N, 99°15′W, *Croat & Hannon 65778* (B, CM, F, GH, K, MEXU, MO, NY, US); *Matuda 26030* (MEXU); *25982* (F, MEXU); *Moore & Bunting 8820* (BH); Barranca Santa Clara, N de Acatlipa, 1450–1550 m, *Vázquez 3094* (MEXU). **Veracruz**: Córdoba–Veracruz, Ejido San José de Gracia, below Peñuelo, ca. 730? m, *Moore & Bunting 8873* (BH, MO).

Philodendron microstictum Standl. & L. O. Williams, Ceiba 3: 108–109. 1952. TYPE: Costa Rica. Puntarenas: Esquinas Forest Reserve, sea level, 10 Jan. 1951, *Allen 5755* (holotype, EAP; isotypes, F, GH, US). Figures 289, 290.

Hemiepiphytic vine, stem scandent, green to gray-green, drying pale yellowish brown, unscented, leaf scars inconspicuous, 1.2 cm long, 8 mm wide, obscured by cataphylls; internodes smooth, semiglossy, 6–12 cm long, 1–2 cm diam., longer than broad, moderately green, drying khaki-colored, epidermis fissured transversely; roots drying light reddish brown, smooth, weakly glossy, 20–30 cm long, 2–3 mm diam., 4–6, at the nodes; cataphylls subcoriaceous, bluntly 2-ribbed or unribbed, pale green to cream-colored, promptly deciduous; **petioles** 12–24 cm long, 2–4 mm diam., subterete to broader than thick to broadly D-shaped, weakly spongy, bluntly flattened to broadly sulcate adaxially, rounded abaxially, with adaxial margins blunt, surface pale or dark green streaked and demarcated from blade by dark green ring around apex; **blades** broadly ovate, moderately coriaceous, abruptly acuminate at apex (the acumen tightly inrolled, 1–4 mm long), weakly subcordate at base, 12.5–30 cm long, 13–21.5 cm wide (0.7–1(1.7) times longer than wide), (0.65–2 times longer than petiole), about equal in length to petiole, broadest ± near the middle, margins straight, upper surface dark green, semiglossy, somewhat pruinose, lower sur-

face glossy to weakly glossy, paler; anterior lobe 12–20.5 cm long, 10.7–22 cm wide (1.85–3 times longer than posterior lobes); posterior lobes 4–8 cm long, 3.5–9.5 cm wide, broadly rounded to obtuse; sinus arcuate, sometimes parabolic, 3.4–6 cm deep; midrib broadly convex to weakly raised, concolorous to paler than surface above, weakly to broadly convex, paler than surface below; basal veins about 3 per side, obscurely and scarcely more conspicuous than primary laterals; posterior rib lacking; primary lateral veins (3)4–5 per side, obscure above; minor veins about as conspicuous as the primary laterals, arising from the midrib only. INFLORESCENCES spreading, as long as leaves, 1 per axil; peduncle 14–25 cm long, 2–6 mm diam., subterete, green; **spathe** 6.5–15 cm long (0.3–1 times longer than peduncle); spathe blade green outside, pale green inside; spathe tube ca. 5 cm long, green outside, red or violet-purple inside; **spadix** sessile, 8 cm long, broadest below the middle; pistillate portion medium green to pale greenish yellow, ± cylindrical, 1.9–2 cm long, 6.5–7 mm diam. at apex, 7–8 mm diam. at middle, 6.5–7 mm wide at base, with 13 (per cm) flowers per spiral; staminate portion 5.9–8.3 cm long; fertile staminate portion white, tapered toward apex, 5–9 mm diam. at base, 5–6 mm diam. at middle, 0.9 mm diam. ca. 1 cm from apex, broadest at the base, mostly narrower than the pistillate and sterile portions; sterile staminate portion broader than the pistillate portion, 6–9 mm diam.; pistils 1.2–1.4 mm long, 0.8–1.1 mm diam.; ovary 6–7-locular, 0.8–1 mm long, 0.8–1.1 mm diam., with sub-basal placentation, walls drying weakly warty; locules 0.8 mm long, 0.3 mm diam., ovule sac 0.7–0.8 mm long; ovules 1 per locule, contained within transparent ovule sac, 0.4 mm long, as long as funicle; funicle 0.4 mm long; style 0.2 mm long, 1 mm diam., similar to style type B; style apex flat; stigma unlobed, subdiscoid to somewhat cylindrical, 0.8–0.9 mm diam., 0.2 mm high, covering almost entire style apex, centered on stylar canal pores; the androecium truncate, margins irregularly to bluntly 4–6-sided, 1.2 mm long, 0.8 mm diam. at apex; thecae ± cylindrical, 0.3 mm wide, ± parallel to one another, contiguous; sterile staminate flowers acutely or bluntly and irregularly 4–6-sided, 1.2–2 mm long, 0.7–1.1 mm wide. INFRUCTESCENCE with fruits whitish. Seeds (dried) ca. 20 per locule, tan, 1–1.2 mm long, 0.5–0.6 mm diam., finely ridged with much finer cross-etching.

Flowering in *Philodendron microstictum* occurs during the dry season and early rainy season, with flowering collections known from January, April, and May, and post-anthesis collections from February, March, May, and July. Immature fruits have been collected in May.

Philodendron microstictum is endemic to Costa Rica (though to be expected on the Burica Península in adjacent Panama), where it is restricted to the Pacific slope, at 50 to 450 m elevation in wetter parts of *Tropical moist forest, Tropical wet forest,* and *Tropical wet forest* basal belt transition life zones.

Philodendron microstictum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by its scandent habit; long, moderately slender stems drying pale yellowish brown; subterete petioles, which are about as long as the blades; and broadly ovate, weakly subcordate blades (which may be as wide or wider than long) with an arcuate sinus and obscure primary lateral and basal veins (sometimes with only the basal veins visible). Also characteristic is the externally green spathe (red within the tube) with the peduncle as long as or longer than the petiole.

Philodendron microstictum is not easily confused with any other species. It has been confused by some with *P. scandens,* which differs in having more narrowly ovate blades with prominent major veins and a spathulate to parabolic sinus, and much more short-pedunculate inflorescences (with the peduncles much shorter than the petioles).

This species is perhaps related to *P. chirripoense,* which is also a vine with inflorescences longer than leaves and has blades of similar color and texture. That species differs in having longer, more slender internodes that dry dark brown and by its narrowly ovate, subcordate blades, which are more than twice as long as broad and have more prominent primary lateral veins.

Additional specimens examined. COSTA RICA. **Puntarenas**: Palmar Norte, 100–200 m, *Croat 35107* (CR, MO); Palmar Norte, along trail to Jalisco, 50–700 m, *Croat 35189* (F, MO); 110 m, *Croat & Hannon 79210* (CR, INB, MO); Villa Neily–San Vito de Coto Brus, Cuesta Fila de Cal, 300 m, 8°41′N, 82°57′W, *Grayum et al. 7580* (CR, MO); El General Valley, Río Angel–Río Volcán, 450–500 m, *Williams et al. 24214* (CR, F); Osa Península, 20–300 m, *Liesner 1836* (B, MO); ca. 5 km W of Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Liesner 7300* (CR, F, MO, PMA); Fila Huacas, ca. 4 km NE of Las Huacas ("Venecia") along road to Sinaí, 450–500 m, 8°52′N, 83°17′W, *Grayum & Hammel 10132* (CR, MO); Parque Nacional Corcovado, La Palma, 100 m, 8°35′N, 83°30′40″W, *Herrera 4066* (CR, L, MO, NY); Sirena, 0–150 m, 8°27–30′N, 83°33–38′W, *Kernan 463* (CR); in Monkey Woods (just W of airstrip), 5 m, 8°29′N, 83°35′W, *Hammel et al. 16643* (CR, MO); Claro Ridge, 1–10 m, 8°28′N, 83°35′W, *Kernan & Phillips 1028* (CR, MO); Sirena Woods, 1–50 m, 8°28′N, 83°35′W, *Kernan & Phillips 1089* (CR, MO); Río Sorpresa, ca. 1 km NE of Golfito, E of microwave towers, ca. 400 m, 8°39′N, 83°10′W, *Croat & Grayum 59941* (CR, MO); Golfito, Cerro Las Torres, 500

m, *G. Herrera 5045* (CR, INB, MO); Reserva Forestal Golfo Dulce, W of Rancho Quemado, 1–300 m, 8°44′N, 83°36′W, *Saborío et al. 127* (INB, MO); Río Volcán, 48 km SE of San Isidro General, 300 m, *Molina et al. 18162* (F, GH, NY, US). **San José**: Río Negro, ZP La Cangreja, ca. 1.5 km E of Santa Rosa de Puriscal, 320 m, 9°42′N, 84°23′30′W, *Grayum et al. 8340* (MO); Parque Nacional, sector Esquinas, vic. Fila Gamba, 200–300 m, *Croat & Hannon 79288* (MO).

Philodendron morii Croat, sp. nov. TYPE: Panama. Panamá: Valle de Madroño, ca. 10 mi. N of La Margarita (near Chepo), in forest S of and on Continental Divide, near border of Comarca de San Blas, along trial to Cangandí, 350–450 m, 9°19′N, 79°08′W, 21 Feb. 1986, *Hammel & McPherson 14530* (holotype, MO–3398570). Figures 291, 292.

Planta epiphytica; internodia 1–1.5 cm longa, 1.5–2 cm diam.; cataphylla 13 cm longa, obtuse 2-costata, decidua; petiolus subteres, 23–37 cm longus, (2)4–6 mm diam., subspongiosus; lamina ovato-triangularis, leniter cordata basi, 25–27.5 cm longa, 11.5–16 cm lata, in sicco canaviridis; inflorescentia 2; pedunculus 9.5–14 cm longus, 3–6 mm diam.; spatha 8.7–12 cm longa, viridis vel flavividis omnino; pistilla (3)4–5(6)-locularia; loculi cum 3–6 seminibus; baccae albae.

Epiphytic; stem appressed-climbing; internodes semiglossy, 1–1.5 cm long, 1.5–2 cm diam., about as long as broad, dark green, drying light brown; roots drying reddish brown; cataphylls 13 cm long, bluntly 2-ribbed, green, deciduous, intact; **petioles** 23–37 cm long, (2)4–6 mm diam., subterete, somewhat spongy, dark green, obscurely flattened adaxially, surface unmarked, often dries with loose, puffy epidermis; **blades** ovate-triangular, narrowly acuminate at apex, weakly cordate at base, 25–27.5 cm long, 11.5–16 cm wide (1.7–2.4 times longer than wide), (0.7–1.2 times longer than petiole), about equal in length to petiole, upper surface semiglossy, lower surface drying green, weakly glossy, moderately paler; anterior lobe 24–28 cm long, 12.6–16 cm wide; posterior lobes broadly rounded, 5–7 mm long, 3–7.5 cm wide, broadly rounded to obtuse; sinus arcuate with blade decurrent on petiole; midrib prominently raised above, slightly paler than surface below; basal veins 2–3 per side, with 0–1 free to base, 0–1 coalesced less than 1 cm; posterior rib weak, to 1.3 cm long, naked throughout its length; primary lateral veins (2)5–8 per side, departing midrib at a 40–50° angle, straight to the margins, sunken and concolorous above, convex and darker than surface below; minor veins fine, numerous, and distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES (post-anthesis) 2 per axil; peduncle 9.5–14 cm long, 3–6 mm diam.; **spathe** 8.7–12 cm long, (0.8–1.1 times longer than peduncle), green to yellowish green throughout; spathe tube 3.5–5 cm long; **spadix** 8–11 cm long; pistillate portion (post anthesis) 5.7 cm long in front, 4.8 cm long in back, 1.5 cm diam. midway, 1.2 cm diam. near apex, 8 mm diam. near base; fertile staminate portion 5 cm long, narrowly tapered to apex, the narrowest portion to 5 mm diam., ca. 1.3 cm above base; sterile staminate portion broader than constricted area, to 5.5 mm diam.; pistils 1.4–1.6 mm long; ovary (3)4–5(6)-locular, with sub-basal placentation; locules 1.3 mm long, 0.5 mm diam.; ovules 1 per locule, 0.3 mm long; funicle 0.2–0.3 mm long (can be pulled free to base), style similar to style type D; style apex flat to weakly rounded, 0.6–0.7 mm long, style boss small; stigma covering entire style apex and inserted on style boss; the androecium truncate, margins irregularly 4–6-sided, 0.7 mm long. INFRUCTESCENCE with pistillate spadix 3–5 cm long; berries white, ± oblong-ellipsoid, 1.1–2 mm long, 0.4–0.8 mm diam.; seeds 3–6 per locule, tan.

Flowering phenology in *Philodendron morii* is poorly known, but it is perhaps bimodal with flowering collections known in March and November and immature fruits in December, February, and June.

Philodendron morii is endemic to Panama, known only from highlands east of the Canal Area in Panamá Province and Comarca de San Blas and from Cerro Pirre in Darién Province, at 450 to 850 m elevation in *Tropical wet forest* and *Premontane rain forest* life zones.

Philodendron morii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. This species is characterized by its slender internodes (about as long as broad); bluntly two-ribbed, deciduous cataphylls; terete petioles (about as long as the blades), which often dry with loose, puffy epidermis; ovate-triangular, scarcely cordate, green-drying blades; and peduncles equaling or exceeding the green spathes.

Philodendron morii is most similar to *P. sphalerum* Schott from the Guianas, which has similar green-drying, long-petiolate leaves. The latter species differs in having the leaf blades acute to rounded or truncate at the base and proportionately longer petioles (fully as long as or much longer than the blades). In addition, *P. sphalerum* has up to four much smaller inflorescences with spathes 5.5–7 cm long, whereas *P. morii* has one to two much larger inflorescences per axil (spathes 9–12.5 cm long). *Philodendron morii* is also similar to *P. wilburii*, especially in terms of size and color of its leaf

blades. The latter species differs, however, in comprising more or less scandent plants with usually long internodes.

Philodendron morii is not easily confused with any other Central American species. It is named in honor of one of its earliest collectors, Scott Mori (NY), who collected for the Missouri Botanical Garden during 1974–1975.

Additional specimens examined. PANAMA. **Darién**: Parque Nacional Darién, W side of Cerro Pirre, 800–1050 m, 7°56′N, 77°45′W, *Croat 68700B* (MO). **Panamá**: Cerro Jefe region, Altos de Azul–Río Chagres, 700–850 m, 9°15′N, 79°30′W, *McPherson 11899* (MO, PMA, US); 3–3.5 mi. NE of Altos de Pacora, 11.1–11.6 mi. beyond Lago Cerro Azul, 700–750 m, 9°15′N, 79°25′W, *Croat 68693* (CM, MO); Campos Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Liesner 567* (MO); Gorgas Memorial Labs "Campamento Quatro," 5–10 km NE of Altos de Pacora, ca. 600 m, *Mori & Kallunki 3441* (MO). **San Blas**: Río Diablo, Cordillera de Ibedón, 350–480 m, 9°21′N, 78°34′W, *Herrera et al. 1489* (MO, PMA, US).

Philodendron niqueanum Croat, sp. nov. TYPE: Panama. Darién: Serranía de Pirre, along headwaters of Río Escucha Ruido, ca. 16 km due N of Alto de Nique, ca. 7°47′N, 77°45′W, 27 July 1976, *Croat 37942* (holotype, MO–2416709). Figures 293–296.

Planta hemiepiphytica; internodia brevia, usque 5 cm diam.; cataphylla incostata vel leniter 1-costata, rubra, persistentia plus minusve intacta; petiolus teres, (32)46–59 cm longus, in sicco 6–8 mm diam.; lamina ovata vel late ovata, (28)42–55.5 cm longa, (14)25–28.5 cm lata, circa tam longa quam petioli; sinus plus minusve V-formatus; inflorescentia immatura; pedunculus 4 cm longus; spathae virides.

Hemiepiphytic; stem scandent when young, appressed-climbing when adult; internodes short, to 5 cm diam. (younger stems with internodes to 8 cm long, 1.5 cm diam.), epidermis moderately smooth, dark reddish brown; cataphylls unribbed to weakly 1-ribbed, red, persisting ± intact; **petioles** (32)46–59 cm long, 6–8 mm diam., terete; **blades** ovate to broadly ovate, acuminate at apex, truncate to subcordate at base, (28)42–55.5 cm long, (14)25–28.5 cm wide (1.7–2 times longer than wide), (ca. 0.9 times the petiole length), about equal in length to petiole, upper surface weakly glossy, drying dark brown, lower surface paler, drying dark yellowish brown; anterior lobe (27)37–49.5 cm long, 25–28.5 cm wide (4.7–5.4(13.5) times longer than posterior lobes); posterior lobes (2)7–9 cm long, 9–12 cm wide, broadly rounded to obtuse; sinus ± V-shaped, to 4 cm deep; midrib prominently raised, paler than surface above, raised below; basal veins 3 per side, with 0 free to base, some of the lowermost coalesced to ca. 1 cm; posterior rib never naked; primary lateral veins 5–9 per side, departing midrib at a 45–65°(70°) angle, weakly arcuate to the margins, sunken above, raised below; minor veins obscurely visible, slightly raised on drying below, arising from the midrib only. INFLORESCENCES immature; peduncle 4 cm long; **spathe** green, 7 cm long; **spadix** immature.

Flowering in *Philodendron niqueanum* is poorly known owing to too few collections overall. The species was collected with flower buds in late July and probably both flowers and fruits within the rainy season (although, since it flowers so late, the fruits may mature in the dry season).

Philodendron niqueanum is endemic to Panama, known only from the type locality on the Serranía de Pirre, at 1530 to 1550 m elevation in *Tropical Lower Montane wet forest.*

Philodendron niqueanum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Ecordata.* This species is characterized by its thick, short internodes; red, weakly one-ribbed cataphylls persisting mostly intact; terete petioles; and narrowly ovate, dark brown-drying blades about as long as the petioles.

Philodendron niqueanum is apparently close to *P. lentii,* which ranges from Costa Rica to central Panama, but no further east than the province of Coclé. Both species are similar in having truncate- to subcordate-based leaf blades with more or less V-shaped sinuses. *Philodendron lentii* differs in having the primary lateral veins sunken, paler, and much more conspicuous on the upper dried blade surface. In contrast, the primary lateral veins of *P. niqueanum* are scarcely or not at all paler than the surface on dried leaves and are raised rather than sunken. In addition, the epidermal pattern is alveolate and moderately smooth at 10× magnification on the upper blade surface of *P. niqueanum,* whereas *P. lentii* lacks an alveolate pattern and the adaxial surface is densely covered with round, pale inclusions.

Philodendron niqueanum is named for the type locality near the Alto de Nique, hence the name.

Additional specimen examined. PANAMA. **Darién**: Cerro Pirre region, ca. 9 km from Alto de Nique, 1480–1520 m, *Croat 37886* (MO, PMA, US).

Philodendron panamense K. Krause, in Engl. & K. Krause, Pflanzenr. IV. 23Db (Heft 60): 65. 1913. TYPE: Panama. Canal Area: at Frijoles, 25–30 m, 9°10′N, 79°48′W, *Pittier 3753* (holotype, US). Figures 297–299.

Usually hemiepiphytic; stem appressed-climb-

ing, to 1.3 m long, sap reddish, sticky; internodes short, semiglossy, 2.5–4 cm diam., sometimes longer than broad, dark green; roots several per node, drying 2–4 mm diam., dark brown, semiglossy, sparsely scaly; cataphylls 18–20 cm long, sharply 1-ribbed to sharply 2-ribbed, green to whitish, drying light brown, persisting briefly ± intact, eventually fibrous, sometimes persisting for a time, eventually deciduous; **petioles** erect-spreading, (23)34–70(79) cm long, 4–13 mm diam., terete to subterete, sometimes weakly flattened or with narrow flattened rib adaxially, sometimes weakly and narrowly sulcate at base, dark green, sometimes pink at base, surface sparsely to densely pale greenish striate or striate-lineate, minutely grooved upon drying, geniculum to 6.5 cm long, sheath 1–4 cm long, usually inconspicuous, to 10 cm long when subtending an inflorescence; **blades** broadly triangular-ovate or more infrequently ovate, subcoriaceous, semiglossy, moderately bicolorous, abruptly acuminate, sometimes acute at apex (the acumen sometimes inrolled, to 4 mm long), deeply cordate at base, 32–72 cm long, 24–38 cm wide (1.2–2.3 times longer than wide, averaging 1.5), ((0.3)0.7–1.4 times longer than petiole, averaging 1.07), broadest near point of petiole attachment; upper surface dark green and glossy, drying semiglossy, dark gray-brown to olive-green, often somewhat blackened, lower surface slightly paler, semiglossy; margins sometimes broadly undulate; anterior lobe 25–41(58) cm long, (15)20–36(41) cm wide (1.9–4 times longer than posterior lobes); posterior lobes 7.5–18 cm long, 4.5–17.7 cm wide, rounded to broadly rounded to broadly obtuse; sinus hippocrepiform to parabolic (arcuate on younger blades), 4–12 cm deep; midrib broadly sunken, concolorous or paler than surface above, weakly asperous, thicker than broad, matte, sometimes short-white-striate, darker than surface below; basal veins 5–8 per side, with 1 free to base or nearly so, third and higher order veins coalesced 4–7 cm long; posterior rib naked for 2–3 cm long; primary lateral veins 4–7 per side, departing midrib at a 55–65° angle, spreading to a 65–75° angle, usually curved down gradually before merging with the midrib, narrowly sunken, concolorous or paler than surface above, convex, matte, slightly darker than surface below; interprimary veins narrowly sunken above; minor veins distinct, darker than surface below, arising from both the midrib and primary lateral veins; secretory ducts moderately visible on lower dried surface, alternating with minor veins. INFLORESCENCES ± erect, 4(6) per axil; peduncle (4.5)6.5–20 (most more than 15) cm long, 4–12 mm diam., pale green, strongly white-lineate, slightly to moderately bent just below the spathe; **spathe** 10.5–18.5 cm long, (0.6–1.7(2.7) times longer than peduncle), acute at apex; spathe blade white outside, (opening 4–7.5 cm wide), pale green, moderately glossy to pale-punctate inside; spathe tube ellipsoid, medium green, densely pale-speckled outside, 6–9 cm long, to 4.5 cm diam., pale green, moderately glossy to pale-punctate inside, **spadix** sessile; protruding forward at anthesis, 12–16 cm long, broadest at upper two-thirds constricted to ca. 1.5 cm diam. between sterile staminate portion and fertile staminate portion; pistillate portion pale green, cylindrical, 3–6.5 cm long in front, 2.7–3.6 cm long in back, 1.3–1.7 mm diam. at apex, 1.3–1.9 mm diam. at middle, 1.1–1.5 mm wide at base; staminate portion 10.5–14.7 cm long; fertile staminate portion creamy white, ± clavate, 1.5–1.8 cm diam. at base, 1.3–2 cm diam. at middle, 9–12 mm diam. ca. 1 cm from apex, about as broad as the pistillate portion; sterile staminate portion 1–1.9 cm diam.; pistils 2.1–3.4 mm long, 1–1.6 mm diam.; ovary 6(7)-locular, 1.5–3.1 mm long, 1–1.6 mm diam., with axile placentation, walls sometimes embedded with granular, crystal-like particles; locules 1.5–3 mm long, 0.5–0.7 mm diam.; ovules 20–31 per locule, 2-seriate, 0.3 mm long; funicle 0.2 mm long, adnate to lower part of partition, style 0.5–0.6 mm long, 1.3–1.6 mm diam., similar to style type B; style apex rounded or domed; stigma truncate, hemispheroid, 1–1.3 mm diam., 0.3–0.5 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins acutely and regularly 4–6-sided, 0.9–1 mm long, 0.7–2.2 mm diam. at apex; thecae oblong to cylindrical, 0.3–0.5 mm wide, ± parallel to one another, contiguous; sterile staminate flowers bluntly, irregularly 4–6-sided, 1.9–4.1 mm long, 1.1–2 mm wide. INFRUCTESCENCE with seeds many per berry, white, narrowly cylindrical, 1.3 mm long, sticky. JUVENILE petioles terete, sheathing broadly, for ½ to ¾ its petiole length, acute to rounded, eventually weakly to strongly cordate; blades broadest at the middle.

Flowering in *Philodendron panamense* occurs during the dry season and early rainy season (March through May), with post-anthesis inflorescences collected from May through August and immature fruits from July through November.

Philodendron panamense is endemic to Panama, but it is likely to occur also in adjacent Colombia. In Panama, it occurs in *Tropical moist forest* on both slopes of the Canal Zone, and *Premontane wet forest* and *Tropical wet forest* in Panamá, Colón, and Da-

rién Provinces, at sea level to 800 m elevation (but mostly below 300 m).

Philodendron panamense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa. Philodendron panamense* is characterized by its appressed-climbing hemiepiphytic habit; short internodes; weakly one-ribbed, mostly deciduous cataphylls (sometimes persisting intact or as fibers); terete, pale-striate petioles; usually broadly triangular-ovate, moderately thin blades with parabolic to hippocrepiform sinus; and by the long-pedunculate spathes with externally greenish tube and white blade (greenish white throughout within). Also characteristic is the peduncle, which is often bent abruptly just beneath the spathe.

This species is most easily confused with *P. lazorii,* which has similar greenish inflorescences. The latter species differs in having more broadly ovate blades (0.97–1.4 times longer than wide and averaging 1.1 times) matte on the lower surface. In contrast, the blades of *P. panamense* are usually ovate-triangular, 1.3 or more times longer than broad (averaging 1.5 times longer) with the lower surface semiglossy. In addition, the peduncles of *P. lazorii* are proportionately shorter and usually shorter than the spathe (vs. often longer than the spathe in *P. panamense*).

Philodendron panamense has been confused with *P. jodavisianum,* which has leaves drying a similar, somewhat blackened color. The latter species differs, however, in having D- to U-shaped petioles, typically with a medial rib adaxially, as well as more typically persistent cataphyll fibers and much shorter peduncles (typically less than 10 cm long in *P. jodavisianum,* vs. typically more than 10 cm long in *P. panamense*). In addition, the peduncles of *P. jodavisianum* are usually straight, not bent.

A collection from the Serranía del Pirre at Cana, *Croat 37600,* is unusual in having several persistent cataphylls and shorter-than-usual peduncles.

Collections from Cerro Sapo and Cerro Pirre (*Croat 55184* and *68951* respectively) differ from typical material of *P. panamense* in having ovate (rather than triangular ovate) leaves and more short-pedunculate inflorescences. In addition, they have sharply two-ribbed cataphylls that persist intact (in the case of *Croat 55184,* on plants in the living collection at MO) or semi-intact (*Croat 68951,* collected in the wild on Cerro Pirre). Most dried collections of *P. panamense* have no cataphylls and longer peduncles.

Earlier (Croat, 1978), the species was reported to be much more widely distributed (to Honduras and Ecuador), but collections from outside of Panama have since proven to be misidentified (most now *P. jodavisianum*).

Additional specimens examined. PANAMA. **Canal Area**: Barro Colorado Island, *Croat 5101* (MO); *5530* (MO); *5840* (F, MO, SCZ); *6188* (MO); *8819* (MO, PMA); *8993* (MO); *9292* (MO, PMA, SCZ); *10083* (MO, SCZ); *10264* (MO, SCZ, US); *10819* (MO); *10894* (MO); *11016* (MO); *14876* (MO); *Bailey & Bailey 199* (BH); Parque Nacional Soberania, Pipeline Road, N of Gamboa, *Luteyn & Foster 1556* (MO); Río Macho bridge, 10 km NW of Gamboa, 115 m, *Nee 7869* (MO, US); 6 mi. N of Gamboa, Río Mendoza, 9°11′N, 79°46′W, *Croat & Zhu 77084* (MO); Summit Gardens, *Croat 10867* (F, MO). **Colón**: Portobelo–Nombre de Dios, 0.5 mi. beyond junction of road to Isla Grande, 9°40′N, 79°35′W, *Croat 49804* (MO); near Nuevo Tonosí, <100 m, *Croat 33517* (MO, RSA). **Darién**: Cerro Sapo, *Croat 55184* (AAU, K, MEXU, MO, PMA, US); ca. 5 km S of Garachiné, Río San Antonio, 130 m, 7°59′N, 78°25′W, *Hammel et al. 1481* (MO); Cerro Pirre region, NW of Cana, 600 m, *Sullivan 672* (MO); vic. of gold mine at Cana, 500–600 m, *Croat 37600* (MO); Serranía Sapo above Casa Vieja along boundary trail of Darién National park, 150–300 m, 7°58′N, 78°23′W, *McPherson et al. 15359* (COL, F, MO, NY, PMA), 550–830 m, *15378* (MO, US); Parque Nacional Darién, vic. of Cerro Pirre base camp, trail E side of Río Paracida, 0–80 m, 8°N, 77°48′W, *Croat 68991* (CM, L, MEXU, MO, PMA, US); Estación Rancho Frío, at N base of Cerro Pirre, ca. 9 km S of El Real, 70–270 m, 8°01′N, 77°44′W, *Hammel et al. 16131* (MO); Cerro Pirre, 800–1050 m, 7°56′N, 77°45′W, *Croat 68951* (CAS, COL, MO, NY, PMA); Río Tuquesa, ca. 2 km air distance from Continental Divide, vic. of Tyler Kittredge gold mine, *Croat 27193* (MO); Parque Nacional Cerro Pirre, Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77100* (CAS, CM, F, MO). **Panamá**: road to Cerro Azul, Mile 5, *Croat 11515* (F, MO, PMA); 720 m, 9°04′N, 79°29′W, *Croat 75152* (CM, MO); Cerro Campana, *Dwyer et al. 4848* (MO), *Croat 12074* (MO, SCZ).

Philodendron pirrense Croat, sp. nov. TYPE: Panama. Darién: Cerro Pirre, middle slopes on western approach, 800–1050 m, 7°56′N, 77°45′W, 29 June 1988, *Croat 68952* (holotype, MO–3610823–24; isotypes, B, COL, F, K, NY, PMA, US). Figures 301–305.

Planta hemiepiphytica aut terrestris; internodia 1–2 cm longa, 4–5 cm diam.; cataphylla 25–30 cm diam., acute 2-costata, persistentia ut fibrae grossae pallidae, cum frustris rubrobrunneis epidermidis; petiolus 56.5–100 cm longus, 5–8 mm diam., aliquantum complanatus adaxialiter cum costa inconspicua; lamina late ovato-cordata, 35–58 cm longa, 27–46 cm lata, in sicco brunnea; costa postica nuda 1–5 cm; inflorescentia 4; pedunculus manifeste albostriatus, 8.5–12 cm longus, 6–8 mm diam.; spatha 12–16.7 cm longa; lamina spathae extus viridis, suffusa marronina, intus alba suffusa marronina; tubo spathae extus rubrimarronino, intus atrimarronino; pistilla 5–6-locularia; loculi 20-ovulati; baccae albae.

Hemiepiphytic or sometimes terrestrial; stem to 5 cm long; internodes short, semiglossy, closely ribbed, completely enclosed in cataphyll fibers,

1–2 cm long, 4–5 cm diam.; roots to ca. 30 cm long, drying reddish brown, smooth, semiglossy, ca. 2 mm diam., closely ridged; cataphylls 25–30 cm long, sharply 2-ribbed (ribs prominently raised), reddish, drying reddish brown, persisting semi-intact, ultimately as coarse pale fibers with fragments of reddish brown epidermis; **petioles** 56.5–100 cm long, 5–8 mm diam., subterete, somewhat flattened near base, weakly flattened toward apex, with faint medial rib adaxially, surface densely short-lineate; **blades** broadly ovate-cordate, acuminate to narrowly acuminate at apex, cordate at base, 35–58 cm long, 27–46 cm wide (1.2–1.5 times longer than wide), (0.6–0.9 times longer than petiole), upper surface drying reddish brown, semiglossy, lower surface much paler; anterior lobe 24.5–48.5 cm long, 27–50 cm wide (1.7–2.3 times longer than posterior lobes); posterior lobes ± rounded, 12.5–19 cm long, 12.5–23.5 cm wide, broadly obtuse; sinus hippocrepiform, 14 cm deep; midrib flat, paler than surface above, drying reddish brown below; basal veins 7–11 per side, with 0–1 free to base, 1–2 coalesced (4)6–8(10) cm, posterior rib well developed, naked for 1–5 cm; primary lateral veins 6–10 per side, departing midrib at a 55–65° angle, ± straight to the margins, prominently sunken above, prominently raised below; interprimary veins distinct, fine, mostly continuous, drying darker than surface below; minor veins arising from both the midrib and primary lateral veins. INFLORESCENCES 4 per axil; peduncle 8.5–12 cm long, 6–8 mm diam., prominently white-striate, clearly demarcated from spathe; **spathe** 12–16.7 cm long (1.3–1.5 times longer than peduncle), moderately constricted above the tube; spathe blade green, tinged maroon, conspicuously and densely pale lineate-striate outside, white, tinged maroon inside; spathe tube red-maroon, inconspicuously short-lineate outside, 4–6 cm long, dark maroon inside; **spadix** sessile; ± ovate, 11–13.4 cm long, broadest below the middle; pistillate portion greenish white, 2.7 cm long, 1.4 cm diam. at apex, 1.3 cm wide at base; staminate portion 10.8 cm long; staminate portion 5.7–8.3 cm long; fertile staminate portion white, tapered toward apex, 1.4 cm diam. at base, 1.3 cm diam. at middle, 8 mm diam. ca. 1 cm from apex, broadest at base, about as broad as pistillate portion; sterile staminate portion broader than the pistillate portion, 1.4–1.5 cm diam., pistils 2.5 mm long, 1.2–1.4 mm diam.; ovary 5–6-locular, 1.7 mm long, 1.3 mm diam., with axile placentation, walls embedded with granular, crystal-like particles; locules 1.7 mm long, 0.4 mm diam.; ovules 20 per locule, 2-seriate, contained within gelatinous matrix (no true envelope), 0.2–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, style 0.3 mm long, 1.3 mm diam., similar to style type B; style apex flat; stigma subdiscoid to slightly hemispheroid, weakly lobed, 1.2 mm diam., 0.1–0.3 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided; thecae oblong, 0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregular, 4–6-sided, 2.1–3 mm long, 1.7 mm wide. Berries white.

Flowering in *Philodendron pirrense* occurs during the early rainy season, judging by post-anthesis collections from June and July.

Philodendron pirrense is endemic to Panama, where it is known for certain only from the Serranía de Pirre, at 1000 to 1560 m elevation in *Premontane rain forest.*

Philodendron pirrense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its short internodes; sharply two-high-ribbed cataphylls persisting as pale fibers with tiny fragments of thin, reddish brown epidermis; petioles somewhat flattened adaxially with a faint medial rib; broadly ovate-cordate blades with a well-developed posterior rib naked to the sinus up to half its length; inflorescences up to four per axil; and whitish peduncles clearly demarcated from the red spathe tube.

Philodendron pirrense is similar to *P. copense,* with which it shares dried leaves of similar color and persistent, reddish brown cataphylls. The latter species differs in having longer blades with the anterior lobes frequently concave along their margins and petioles with a yellowish or reddish brown flaking periderm.

Additional specimens examined. PANAMA. **Darién**: Serranía de Pirre, ca. 12 km N of Alto de Nique, 1520–1560 m, *Croat 37916* (MO); ca. 9 km from Alto de Nique, 1480–1520 m, *Croat 37887* (MO); Río Escucho Ruido, ca. 16 km N of Alto de Nique, 1530–1550 m, *Croat 37944* (MO).

Philodendron platypetiolatum Madison, Selbyana 2: 22. 1977. TYPE: Ecuador. Los Ríos: Río Palenque Science Center, km 56 on road to Santo Domingo and Quevedo, 150–220 m, ca. 0°35′S, 79°22′W, *Dodson 6638* (holotype, SEL; isotypes, MO, QCA, US). Figures 306–308.

Hemiepiphytic; stem ± scandent, loosely appressed-climbing, to 3 m long, semiglossy, sap clear, watery, sticky, leaf scars to 2 cm wide; internodes slender, 14–20 cm long, 1–2 cm diam., longer than broad, sometimes somewhat flattened on

side above, semiglossy, green to grayish green, epidermis drying tannish brown, cracking, loosening and flaking; roots pale to brownish, less than 20 cm long, thin, 2 mm diam., smooth; cataphylls (6)10–17 cm long, sharply 2-ribbed, sharply and deeply sulcate with margins flared, pale to medium green, drying yellowish to olive-green, deciduous; **petioles** 15.5–56 cm long, 3–9(12) mm diam., broadly flattened to markedly flattened and turned slightly upward adaxially, broadly convex abaxially, firm, medium to dark green, surface ± unmarked; **blades** ovate-triangular to broadly ovate, subcoriaceous, semiglossy to glossy, weakly to moderately bicolorous, acuminate, sometimes long, narrowly acuminate at apex (the acumen tightly inrolled, 2–3 mm long), weakly cordate at base, 17–39 cm long, 12.7–29 cm wide (1–1.5 times longer than wide), (0.6–1.4 times longer than petiole), usually about equal in length to petiole; anterior lobe 15–34 cm long, 13–29 cm wide (2.4–4.5(5.2–5.4) times longer than posterior lobes); posterior lobes 4–10 cm long, 5–12 cm wide, broadly rounded to obtuse; sinus hippocrepiform, rarely arcuate with blade decurrent on petiole; midrib sunken or flat to broadly convex above, slightly paler than surface to concolorous above, bluntly low-triangular to convex below, paler than surface below; basal veins (2)3–4(5) per side, with 0–1 free to base, second and third coalesced 1–2 cm; posterior rib naked for 0–1 cm; primary lateral veins 3–5 per side, departing midrib at a 50–60° angle, straight to the margins, sunken to weakly sunken above, convex below; minor veins moderately indistinct, arising from both the midrib and primary lateral veins. INFLORESCENCES 1(2) per axil; peduncle 5–20 cm long, 2–11 mm diam., subterete or bluntly 1–2-angled, pale green, semiglossy, unmarked; **spathe** semiglossy, (8)11–18 cm long (0.7–2(2.8) times longer than peduncle); spathe blade green or red outside, pale yellow-green (dark red in South America), inside; spathe tube green to olive-green, usually tinged red or maroon outside, 4.5–7.5 cm long, tinged red or maroon inside; **spadix** sessile; weakly tapered, ± acute at apex, 8–9.8 cm long, broadest at the base or ± uniform throughout, constricted weakly between sterile and fertile staminate portions; pistillate portion pale greenish, cylindrical or weakly tapered toward the apex, 2.5(3.5) cm long, 9–11 mm diam. at apex, 10–13 mm diam. at middle, 10–13 mm wide at base; staminate portion 5.7–7.3 cm long; fertile staminate portion white, weakly tapered or cylindrical, 5–7 mm diam. at base, 4–5 mm diam. ca. 1 cm from apex, broadest at the base or ± uniform, narrower than the pistillate portion, broader than or as broad as the sterile portion; sterile staminate portion as broad as or slightly narrower than the pistillate portion, 5–10 mm diam.; pistils (0.8)1.7–2.5 mm long, (0.6)0.9–1.4 mm diam., white; ovary (6)7–8-locular, (0.7)1.1–1.8 mm long, 0.8–1.2 mm diam., with sub-basal placentation; locules 0.7–1.5 mm long, 0.3 mm diam., ovule sac 0.8 mm long; ovules 3 per locule, 1-seriate, contained within translucent to transparent, gelatinous envelope, (0.2–0.3)0.4–0.5 mm long, longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style (0.1)0.4–0.7 mm long, 0.6–0.8 mm diam., similar to style type B; style apex steeply sloping, sometimes with small medial depression; stigma subdiscoid to hemispheroid, somewhat cupullate, 0.7–0.9(1.3) mm diam., 0.2–0.3 mm high, covering entire style apex; the androecium prismatic, truncate, oblong, margins irregularly 4–6-sided, sometimes weakly scalloped; thecae cylindrical to oblong, 0.3–0.4 mm wide, ± parallel to one another, sometimes ± contiguous; sterile staminate flowers irregularly 4–6-sided or rounded, 0.9–1.5 mm long, 0.7–1.2 mm wide. INFRUCTESCENCE turning red outside; berries green (immature).

Flowering in *Philodendron platypetiolatum* occurs in the early rainy season, June and September, in Central America based on the few available flowering collections. Post-anthesis collections from Costa Rica and Panama are mainly from August through November, but also from March. Immature fruits have been collected only in January, February, and November. Ecuadorian populations have a similar phenology, but flowering collections have been made earlier, in March and April, with post-anthesis collections from March through August.

Philodendron platypetiolatum ranges from Nicaragua to Ecuador, from sea level to 1500 (though most collections are from below 400) m elevation, in *Premontane wet forest, Tropical wet forest* transition to *Premontane wet forest,* and *Tropical wet forest* life zones. This species has been collected at several localities in Choc6 and Valle Departments; in Ecuador, it has only been collected at and near the type locality.

Philodendron platypetiolatum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium.* This species is characterized by its scandent habit; moderately long, slender internodes with tannish brown, frequently flaking epidermis; markedly flattened petioles about as long as the blade; and ovate-triangular to broadly ovate, weakly cordate blades. Though the spathes may be entirely green outside, they usually are heavily tinged with red or maroon outside and the tube within is likewise colored.

There are no other species in Cental America with which *P. platypetiolatum* might be confused. Madison compared this species to *P. lechlerianum* Schott, a species from Peru and Bolivia that has terete petioles.

In Panama, this species ranges along the Atlantic slope but may also occur on the Pacific slope near the Continental Divide. In Ecuador, it is restricted to the Pacific slope.

Ecuadorian specimens have blades that are more broadly ovate than those from Panama, but no other differences have been detected.

Additional specimens examined. COSTA RICA. **Alajuela**: Upala Road, 3 km NNE of Bijagua, 450 m, 10°45′N, 85°3′W, *Burger & Baker 9890* (CR, F, MO, NY, SEL); 5 km S of Canalete, near Río Zapote, 100–200 m, 10°48′N, 85°2′W, *Burger & Baker 9972* (F, MO); Dos Ríos, 5 km S de Brasilia, Río Pizote, 500 m, 10°55′N, 85°20′W, *Herrera 1001* (CR, MO, SAR); 17 km NW of San Ramón, 785 m, 10°14′14″N, 84°33′W, *Croat 68136* (F, MO); Bajo Rodríguez–La Tigra, vic. of La Tigra, 330 m, 10°22′N, 84°38′W, *Croat 68205* (B, CM, G, M, MO, SAR, US); Monteverde Cloud Forest Nature Reserve, Río Peñas Blancas, 1250–1350 m, 9°17′N, 84°86′W, *Burger et al. 10745* (F, MO); Vara Blanca–Puerto Viejo, 3 mi. N of San Miguel, 380 m, *Croat 35666* (MO); Cañas–Upala, 13.8 km N of Bijagua, 100–150 m, *Croat 36433* (MO); 4 km NNE of Bijagua, ca. 400 m, *Croat 36269* (MO); slopes of Miravalles, above Bijagua, *Gómez et al. 19066* (MO); Naranjo–Aguas Zarcas, along Hwy. 15, 8.5 km NE of Villa Quesada, 600 m, *Croat 46973* (CR, MO). **Heredia**: "Starkey Road," 4.5 km SE of bridge at Puerto Viejo, ca. 50 m, 10°26′N, 83°58′W, *Stevens 13489* (MO); La Selva Field Station, *Grayum 2228* (MO); 100 m, *McDowell 329* (MO); 100 m, *647* (CAS); 50–80 m, 10°26′N, 84°01′W, *Grayum 7665* (CR, MO); 6 km from Río Peje crossing, 5 km SSE of Magsasay, 340 m, 10°21′N, 84°04′W, *Schatz & Grayum 634* (CR, MO); Puerto Viejo de Sarapiquí, 100 m, *Croat 44248* (MO); 10°26′N, 84°01′W, *61213* (MO); Parque Nacional Braulio Carrillo, Río Peje–Río Sardinalito, Volcán Barva, 700–800 m, 10°17′30″N, 84°05′W, *Grayum & Herrera 7908* (CR, F, MO, VEN). **Limón**: Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson 6744* (RSA), *Davidson & Donahue 8383* (F, MO, RSA); *Davidson & Donahue 8802* (MO); *8874* (MO, RSA); Barra del Colorado, 0–2 m, 10°47′N, 83°35′W, *Stevens 24214* (CR, MO); Cerro Coronel, 20–170 m, 10°41′N, 83°38′W, *Stevens 24623* (CR, MO); Quebrada Danta, W of Guápiles, 360 m, 10°12′N, 83°49′W, *Croat 68426* (MO, NY); Braulio Carrillo–Guápiles, 250–270 m, *Croat 78744* (CR, INB, MO); Río Colorado, 14 km by air SW of Barra del Colorado, 10–120 m, 10°40′N, 83°40′W, *Davidse & Herrera 31060* (CR, MO); 16 km by air SW of Barra del Colorado, 10°39′N, 83°40′40″W, *31211* (MO). **Puntarenas**: Osa Península, Piedras Blancas, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67687* (CR, K, MO); Rincón de Osa-Esquinas, 100 m, *Pennington et al. 11386* (K); Fila Gamba, ca. 6 km from Golfito airport, <100 m, 8°41′30″N, 83°12′W, *Croat 59926* (CM, K, MO); 200–300 m, *Croat & Hannon 79290* (MO). **San José**: El General Valley, Finca Volcán Angel, *Schubert & Rogerson 769* (A, GH); Braulio Carrillo National park, 600–700 m, *Croat 78778* (CR, INB, MO). NICARAGUA. **Río San Juan**: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23496* (MO). **Zelaya**: Río Sucio, E of Bonanza, ca. 140 m, 14°01′N, 84°34′W, *Stevens 12347* (MO); Mpio. Siuna, Comarca Danlí, 100–130 m, *Ortiz 218* (MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, 9.4 mi. N of Continental Divide, 175 m, 8°46′N, 82°16′W, *Croat 66822* (AAU, MO). **Colón**: Río Guanche, ca. 3–4 km above bridge on road to Portobelo, *J. Witherspoon & F. Witherspoon 8662* (CAS, MO); Sabanitas–Portobello, Río Piedras Lumber Road, 6.7 mi. E of Sabanitas, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75166* (MO, PMA). **Darién**: Parque Nacional Cerro Pirre region, Cana, 500–600 m, *Croat 37661* (MO); near station along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77116* (MO); Parque Nacional Darién, Río Topalisa–Río Pucuro, ca. 17 km E of Pucuro, Mi Casita–La Laguna, 600–850 m, 8°03.5′N, 77°17′W, *de Nevers et al. 8337* (CAS, MO); ca. 5 km E of Pucuro, Quebrada Maskia, 200 m, 8°01′N, 77°25′W, *Hammel et al. 16167* (MO). **Panamá**: El Llano–Cartí, 13.8 km N of Pan-American Highway, *Folsom et al. 5788* (MO); Mile 6.8, 350 m, *Croat 49125* (MO, PMA); Cerro Jefe region, 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76645* (MO); 4.6 km beyond peak on road to Altos de Pacora, ca. 600 m, *Croat 35936* (MO); near summit, 750–800 m, 9°14′N, 79°22′W, *Croat 67083* (MO); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68680* (CM, MO). **San Blas**: El Llano–Cartí Road, vic. Nusagandi, 300–350 m, 9°15′N, 79°W, *Croat 69278* (CM, MO); 450 m, 9°18′N, 79°59′W, *Croat 75118* (CAS, MO, NY, PMA); 10.1 mi. N of main highway, 300 m, 9°20′N, 79°W, *Croat & Zhu 76539* (CM, M, MO); Mile 9, 350 m, 9°20′N, 79°W, *Croat 76999* (MO); Río Playón Chico, 80–200 m, 9°13.5′N, 78°15′W, *Herrera & Arosemena 1778* (AAU, COL, CR, K, MEXU, MO, NY, P, PMA, STRI, US).

Philodendron pseudauriculatum Croat, sp. nov. TYPE: Panama. Panamá: El Llano–Cartí road, 4 mi. from Inter-American Hwy. near El Llano, ca. 300 m, 27 Mar. 1976, *Croat 33730* (holotype, MO–2381528; isotypes, PMA, RSA, SEL). Figures 35, 300, 309, 310, 313, 314.

Planta hemiepiphytica; internodia 1.4(9) cm longa, 2–4 cm diam.; cataphylla 18–27 cm longa, acute 2-costata, decidua; petiolus subspongiosus, 11–42 cm longus, 0.7–2.6 cm diam., subteres, leviter complanatus adaxialiter, late et obtuse sulcatus in medio, cum annuluo viridi apice; lamina oblongo-elliptica vel oblanceolato-elliptica, plurumque acuta vel anguste rotundata, interdum subcordata truncata basi, 27–80 cm longa, 7.5–25 cm lata; in sicco atricaniviridis; inflorescentia 2–3; pedunculus 5.5–21(25) cm longus, 8–12 mm diam.; spatha (10.6)12–23 cm longa, omnino alba vel subrosea, marginibus cremeis; lamina spathae extus eburnea vel flaviviridi, striata flaviaurantiaca, intus pallide viridi vel alba; tubo spathae extus vel atriviridi, interdum extus leniter suffuso purpurascenti secus margines, vivide rubriviolaceo vel atrimarronino vel flaviaurantiaco; pistilla 5–8(9)-locularia; loculi 1–2(4)-ovulati; baccae aurantiacae.

Hemiepiphytic; stem appressed-climbing, to 1 m long; internodes gray-green, glossy to semiglossy,

1–4(9) cm long, 2–4 cm diam., usually somewhat flattened on one side, frequently with a short series of transverse ridges just below the nodes on both sides of the rounded portion of internodes, usually about as broad as long, or broader than long on flowering plants, sometimes slightly longer than broad; roots dark brown, slender, few per node; cataphylls moderately spongy, 18–27 cm long, sharply 2-ribbed (ribs to ca. 1 cm high), medium green, densely dark green short-lineate, deciduous, apiculate (apiculum >1 cm long) at apex. LEAVES erect, ± rosulate, somewhat clustered at or near stem apex; **petioles** 11–42 cm long, 0.7–2.6 cm diam., subterete, somewhat spongy, slightly flattened, bluntly and broadly sulcate midway, less so toward apex, more so toward base adaxially, surface medium green, semiglossy, with dark green ring around apex; **blades** oblong-elliptic to oblanceolate-elliptic, subcoriaceous to coriaceous, somewhat to markedly bicolorous, semiglossy, acuminate, sometimes long-acuminate at apex, mostly acute to rounded, sometimes broadly subcordate, or sometimes truncate at base, 27–80 cm long, 7.5–25 cm wide (2.2–4(5) times longer than wide), (0.97–3.6 times longer than petiole), upper surface dark green, drying dark gray-green, lower surface much paler, yellow-green, drying yellow-green to yellow-brown; sinus (when present) to 2.5 cm deep; midrib flattened at base, slightly sulcate midway, broadly convex at apex and concolorous above, convex, short-green-lineate, paler than surface below; basal veins (0)1–3(4), all free to base; posterior rib lacking; primary lateral veins 8–14 per side, departing midrib at a 65–75° angle (45–55° angle at apex), ± straight to the margins, sunken above, convex and slightly paler than surface or darker than surface below; interprimary veins flat, darker than surface below; minor veins moderately distinct and fine below, arising from both the midrib and primary lateral veins. INFLORESCENCES 2–3 per axil; peduncle 5.5–21(25) cm long, 8–12 mm diam., pale to medium green, finely white- or dark-striate; **spathe** (10.6)12–23 cm long, 1.7 cm diam. (0.7–2.6 times longer than peduncle), constricted midway above the tube, white to pinkish throughout, margins cream; spathe blade creamy white to yellowish green with faint green tinge along center on backside (B & K yellow-red 7.5/9), yellow-orange striate outside, 8.5–9 cm long (opening elliptic in face view, 7.5–9 cm long, 2–5.5 cm wide), pale green to white inside; resin canals orange; spathe tube oblong-ellipsoid, medium to dark green, sometimes weakly tinged purplish along margins outside, densely short white-lineate, semi-glossy outside, 5.5–10.5 cm long, 1.8–4 cm diam., bright red-violet to dark maroon (weakly so toward apex) to yellowish orange, sometimes broad, white-lineate or orange striate inside; **spadix** weakly stipitate to 3–5 mm long, cylindrical to weakly tapered, 7.5–15.3 cm long, broadest below the middle; pistillate portion cylindrical to clavate, pale lime green to pale yellow to medium or dark green, 3–5.5 cm long in front, 1.7–4 cm long in back, 1–1.2 cm diam. at apex, 1.5 cm diam. at middle, 8–11 mm wide at base; staminate portion 4.5–10.7(12) cm long; fertile staminate portion broadest in middle, slightly tapered toward both ends and broadened before the sterile portion, 9–16 mm diam. at base, 9–10 mm diam. at middle, 5–10 mm diam. ca. 1 cm from apex, broadest at the base, as broad as the pistillate portion, narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, white, 8–15 mm diam.; pistils 1.7–3.2 mm long, 1.3–2 mm diam.; ovary 5–8(9)-locular, 1.4–2.3 mm long, 1.5–2 mm diam., with sub-basal placentation, walls embedded with granular, crystal-like particles; locules 1.4–2.1 mm long, 0.3–0.5 mm diam.; ovule sac 1–1.2 mm long; ovules 1–2(4) per locule, contained within transparent, gelatinous ovule sac, 0.4–0.5 mm long, longer than funicle; funicle 0.1–0.5 mm long (can be pulled free to base), style 0.4–1.4 mm long, 0.9–2.1 mm diam., similar to style type B; style apex sloping to rounded, with small medial depression; stigma brush-like, cupulate, subdiscoid, 0.9–1.2 mm diam., 0.2–0.6 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 1.3–1.4 mm long, 1.6–1.8 mm diam. at apex; thecae oblong to cylindrical, 0.4–0.5 mm wide, nearly contiguous and ± parallel to one another; pollen ellipsoidal to spheroidal, <1 mm long, <1 mm diam.; sterile staminate flowers irregularly 4–5-sided, margins bluntly rounded, 1.2–1.9 mm long, 1.8 mm wide. Berries orange (mature) or white; seeds 5 per berry, 1.3–1.9 mm long, 0.5–0.7 mm diam.

Flowering in *Philodendron pseudauriculatum* occurs during the dry season and the first half of the rainy season (January through September). Immature fruits have been collected during March, June, and July, with mature fruits known only from September.

Philodendron pseudauriculatum is definitely known only from Panama and adjacent Colombia (N Antioquia), ranging from 20 to 1400 m elevation in *Premontane wet forest* and *Tropical wet forest* life zones. Most collections have been made at La Mesa (Coclé), Cerro Campana (Panamá), and along the El Llano–Cartí Road (Panamá), but the species is

also known from a single collection in Bocas del Toro and in the Serranía de Cañasas along the Pacific Ocean.

Philodendron pseudauriculatum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum*. This species is recognized by its appressed-climbing habit; short internodes; more or less rosulate habit; somewhat spongy, subterete petioles; oblong-elliptic to oblanceolate-elliptic, dark gray-green-drying blades with mostly narrowly rounded bases, and two to three inflorescences per axil; and white to pinkish spathes clearly demarcated from the peduncles.

Philodendron pseudauriculatum is most easily confused with *P. ligulatum*, especially *P. ligulatum* vars. *heraclioanum* and *ligulatum*, which have similarly shaped blades. *Philodendron ligulatum* var. *heraclioanum* differs in having sharply D-shaped petioles with undulate-margined wings. While the aforementioned varieties of *P. ligulatum* differ in their usually vining habit and typically elongate internodes, these features are particularly apparent in *P. ligulatum* var. *ligulatum*, which has internodes much longer than wide (vs. about as long as broad or scarcely longer than broad as in *P. pseudauriculatum*). In addition, the leaves of *P. ligulatum* frequently dry much darker, mostly somewhat blackened, rather than the typical yellowish or brownish green of *P. pseudauriculatum*. Another feature separating live material of the species is the line of demarcation at the apex of the petiole, which is purple in *P. ligulatum* rather than green as in *P. pseudauriculatum*.

Philodendron pseudauriculatum may also be confused with both *P. auriculatum* (hence the epithet "pseudauriculatum"), from the Pacific slope of southwestern Costa Rica and *P. wendlandii* Schott from the Atlantic slope of Costa Rica and Panama. *Philodendron auriculatum* is distinguished by having leaf blades drying a paler yellow-green color and more narrowed toward the base with minute narrow auriculate posterior lobes. It also has proportionately somewhat longer petioles. *Philodendron wendlandii* differs in having a much shorter stem and petioles typically broader than thick with sharp margins.

Two collections (*Croat 16908* and *Knapp & Mallet 4658*) from San Blas at Puerto Obaldía are probably also this species. They differ in having broader blades and drying somewhat blacker. If these prove to represent *P. pseudauriculatum*, the species is most assuredly present in adjacent Chocó. A collection from the Department of Santander in Colombia at 1460 to 1700 m (*García-Barriga & Jaramillo 19671*) may also be this species.

Additional specimens examined. PANAMA. **Bocas del Toro**: Quebrada Huron, Duwebdulup Peak, N of Río Terebe, 300–900 ft., *Kirkbride & Duke 558* (MO). **Canal Area**: Summit Gardens, *Croat 10791* (F, MO, SCZ). **Coclé**: El Valle region, La Mesa, 650–710 m, *Mori et al. 1916* (MO); *Luteyn & Kennedy 1660* (DUKE); *Hammel 3844* (MO); 860–900 m, *Croat 37420* (MO); 900 m, *22964* (MO); *14362* (MO); 800 m, *Croat & Zhu 76692* (MO); *Bartlett & Lasser 16694* (F, MICH, MO); *Kennedy et al. 3189* (MO, PMA); 785 m, 8°37′N, 80°08′W, *Croat 67112* (MO); summit of Cerro Caracoral, near La Mesa, N of El Valle de Antón, 1100 m, *Knapp 1118* (K, MO); Río Cascajal, Penonomé–Coclecito, 5.6 mi. N of Llano Grande, 150 m, 8°46′N, 80°27′W, *Croat 67484* (AAU, CAS, COL, F, L, MEXU, MO, NY, PMA, QCA, TEX). **Colón**: near Peluca, on road to Nombre de Dios, *Kennedy 2774* (F, MO); Portobelo–Nombre de Dios, Nuevo Tonosí, <100 m, *Croat 33526* (CM, COL, K, L, MO, NY, PMA, QCA, RSA, US); Sabanitas–Portobelo, Río Piedras drainage, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75160* (MO); Portobelo, *Croat & Porter 15606* (MO); Río Boquerón, near No. 1 (manganese mine), E of Salamanca, 50 m, 9°35′N, 79°32′W, *Knapp et al. 5832* (B, K, MO); Puerto Pilón–Portobelo, ca. 1.5 mi. above bridge, <100 m, 9°27′N, 79°4′W, *Croat & Zhu 76251* (CR, MO, PMA); Río Guanche, 30–100 m, *Croat 79322* (PMA); ca. 5 km upstream from road to Portobelo, 50 m, 9°30′N, 79°40′W, *Hammel & Trainer 14765* (MO); ca. 3–5 km above bridge, 50–200 m, *Croat 37002* (MO); 10–100 m, *26147* (BR, F, MO); ca. 50 m, ca. 9°30′N, 79°40′W, *McPherson 8507* (MO); Río Iguanita, near bridge along Portobelo Road, <50 m, 9°27′N, 79°42′W, *Croat 49778A* (MO); Río Miguel de la Borda, vic. of Guásimo, *Croat 9985* (MO, SCZ); Río Sirrí, Trinidad Basin, 20–50 m, *Pittier 4015* (US). **Darién**: Cerro Pirre National Park, W side of Cerro Pirre, base camp, 50 m, 8°N, 77°48′W, *Croat 68962* (M, MO, NY, US); near station along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77094* (CM, MO); Cerro Pirre region, trail NW of Cana, 600 m, *Sullivan 712* (MO); Cana, near Río Setigandí, 540–580 m, *Gentry et al. 28542* (MO); Cana gold mine, vic. of airstrip, 480 m, *Croat 38038* (MO); 500–600 m, *37595* (MO), along Río Cana, SW of Cerro Pirre, 1400 m, *Croat 27292* (MO); Río Coasi, 0–2 mi. E of Tres Bocas, *Kirkbride & Duke 1203* (MO, NY); Río Cocalito, *Whitefoord & Eddy 224* (BM); *162* (BM, MO); Río Jaqué Valley, Quebrada Luka, 100–200 m, 7°27′N, 78°05′W, *Knapp & Mallet 3199* (MO, NY); Río Tuquesa, ca. 2 km by air from Continental Divide, *Croat 27160* (F, MO); *Clezio 168* (MO). **Panamá**: El Llano–Cartí Road, 5 mi. from Pan-American Highway, 350 m, *Croat 67345* (CAS, MO); Km 8–12, ca. 400–450 m, *Nee et al. 8802* (MO); ca. Mile 8, 225–275 m, 9°15′04″N, 79°00′04″W, *McPherson 10492* (AAU, MEXU, MO); Km 19.1, 350 m, 9°19′N, 78°55′W, *de Nevers et al. 7342* (MO); Río Terabe Valley, El Llano–Cartí, 8 km from highway, 300–400 m, 9°16′N, 79°W, *Knapp & Schmalzel 5493* (MO); area around Pilota de Toro, *Folsom et al. 6819* (MO, PMA); Tortí–Pilota del Toro, above Tortí Arriba, *Folsom et al. 4993* (MO, PMA); Cerro Campana, 6.1 mi. above Pan-American Highway, 800 m, 8°41′N, 79°56′W, *Croat 74762* (F, MO); ca. 1 mi. from highway, ca. 150 m, *35991* (MO); along trail to summit, 780–875 m, *25253* (MO, NY, PMA, US); ca. 850 m, 8°42′N, 79°56′W, *Miller et al. 754* (MO); upper slopes, 207 m, *LeDoux 2595* (MO); above Su Lin Motel, *Porter et al. 4250* (MO); Río Tortí, base of Serranía de Cañazas, ca. 15 km SW of Caaza, 150 m, 8°52′N, 78°22′W, *Stein 1342* (MO); Sendero de Interpre-

tación, 1 km al este del Campamento de los guardabosques de INRENARE, 800–900 m, 8°40′N, 79°55′W, *Correa & Montenegro 10681b* (STRI). **San Blas**: El Llano-Cartí Road, Km 19, 350 m, 9°19′N, 78°55′W, *de Nevers et al. 5598* (MO); Puerto Obaldía, 0–50 m, *Pittier 4398* (US); beach E of Puerto Obaldía, *Croat 16908* (MO); Puerto Obaldía–La Bonga, ca. 2 hours walk from Puerto Obaldía, 0–50 m, 8°40′N, 77°25′W, *Knapp & Mallet 4658* (MO); Nusagandi, El Llano–Cartí Road, 10.1 mi. N of main highway, 300 m, 9°20′N, 79°W, *Croat & Zhu 76554* (CM, MO); Río Playón Chico, 80–200 m, 9°13′05″N, 78°15′W, *Herrera & Arosemena 1784* (MO, PMA, STRI).

COLOMBIA. **Antioquia**: Mpio. Turbo, carretera tapón del Darién, sector Río León–lomas aisladas, km 37, 20 m, *Brand 1070* (COL, MO). **Chocó**: Mecana, N of Bahía Solano, 1–100 m, 6°16′N, 77°21′W, *Juncosa 1609* (MO). **Risaralda**: Mistrató, Jeguadas–Santa Cecilia, 800–850 m, 5°24′N, 76°01′W, *Betancur et al. 3459* (MO); corregimiento de Santa Cecilia, 500–550 m, 5°17′N, 76°13′W, *Betancur et al. 2930* (MO); Pueblo Rico, Santa Cecilia–Pueblo Rico, Km 13, Quebrada Pionda, 700–900 m, 5°17′N, 76°13′W, *Betancur et al. 3052* (MO).

Philodendron pterotum K. Koch & Augustin, in A. Braun et al., Append. gen. sp. Hort. berol. 1854: 6. 1854–1855. TYPE: Cultivated at Berlin [received from Warszewicz in Venezuela] (holotype, B? lost). Panama. Canal Area: vic. Fort Sherman, along road between Gatún Locks and Fort Sherman, ca. 3 mi. W of Gatún Locks, <50 m, 9°19′N, 79°57′30″W, 17 July 1994, *Croat & Zhu 76982* (neotype, MO–4619421–26, here designated; isoneotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GB, GH, K, MEXU, P, PMA, QCA, RSA, SEL, VEN, W). Figures 311, 312, 315, 316.

Philodendron mirificum Standl. & L. O. Williams, Ceiba 3: 38. 1952. TYPE: Costa Rica. Puntarenas: near Palmar Sur de Osa, 75 m, 24 Mar. 1951, *Allen 6031* (holotype, EAP; isotype, F).

Usually hemiepiphytic or epiphytic; stem appressed-climbing, semiglossy, sap watery, weakly turpentine-scented, leaf scars conspicuous, 2 cm long, 1 cm wide; internodes sometimes obscured by cataphylls, sparsely short-striate, about as long as broad or sometimes longer than broad, 2–8 cm diam., dark green to gray-green, eventually brown, epidermis sometimes cracking, fissured longitudinally; roots short, few per node; cataphylls 20–30 cm long, sharply 2-ribbed, C-shaped, semiglossy, dark green, densely pale lineate, persisting as reddish brown, semi-intact fibers, eventually deciduous; **petioles** (37)47–111 cm long, (3–5)6–13(16–22) mm diam., erect-spreading, D-shaped, marginally winged, broadly convex adaxially, with adaxial margins slender, erect, undulate, medium green, weakly glossy, conspicuously pale striate; sheath with margins involute; **blades** ovate, subcoriaceous, semiglossy, moderately bicolorous, abruptly acuminate at apex (the acumen inrolled, 2–4(6) mm long), broadly cordate at base, 36–93 cm long, 22–84 cm wide (0.7–1.5(2.9) times longer than wide), (0.6–0.9 times the petiole length), margins weakly undulate, upper surface dark green, lower surface much paler, glossy, drying yellow-green; anterior lobe 23.5–65(84) cm long, 22.1–75(86.4) cm wide (1.1–2.8 times longer than posterior lobes); posterior lobes 12–33 cm long, (11)15–34 cm wide, directed inward, broadly rounded to broadly obtuse; sinus spathulate to rhombic; basal veins 7–10 per side, first free to base, part of remainder coalesced 1–6 cm, loosely so distally; posterior rib naked to 6 cm; midrib flat to broadly sunken, paler than surface above, convex to narrowly rounded, paler than surface below; primary lateral veins 3–6 per side, departing midrib at a 45–55° angle, ± straight to weakly arcuate to the margins, deeply sunken, paler than surface above, raised to convex, paler than surface below; interprimary veins weakly raised, darker than surface below; the minor veins moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2–4 per axil; peduncle (2)4–12 cm long, 4–13 mm diam., medium green, coarsely white streaked toward apex; **spathe** 11–29 cm long (1.4–3.8(5) times longer than peduncle), ± cuspidate at apex; spathe blade light green outside, greenish white inside; spathe tube abruptly delineated from tube, reddish to purplish to dark purple-violet (B & K purple 2/10) or dark green and raised-white-striate at base outside, red to magenta inside; **spadix** weakly stipitate, exserted from the spathe, constricted above sterile staminate portion; pistillate portion pale green, 4.3 cm long in front, 3.8 cm long in back, 2 cm diam. at apex, 1.7 cm wide at base; staminate portion 16–18 cm long; fertile staminate portion white, 1.7 cm diam. at middle; sterile staminate portion 1.4–2.2 cm diam.; pistils 2.2–2.8 mm long, 1.1–1.4 mm diam.; ovary 6-locular, with axile placentation; locules 1.5–1.9 mm long, 0.4 mm diam.; ovules ca. 20 per locule, 2-seriate, somewhat translucent, 0.2–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition, style similar to style type B; style apex flat to weakly rounded; stigma subdiscoid to weakly hemispheroid, sometimes weakly lobed, 1.5 mm diam., 0.5 mm high, covering entire style apex; the androecium truncate, prismatic, margins irregularly 4–6-sided, 0.7–1.5 mm long; thecae oblong, 0.4 mm wide, not contiguous, ± parallel to one another; sterile staminate flowers irregularly 4–5-sided, 1.5–2.5 mm long. INFRUCTESCENCE with spathe green at base and tip, pur-

ple around fruiting area when ripe, berries pale brown to white. JUVENILE and PRE-ADULT plants with petioles flattened adaxially; blades broadly ovate. PRE-ADULT blades broadly ovate, 28.5 cm long, 22.5 cm wide.

Flowering in *Philodendron pterotum* occurs in the early rainy season from May through August based on both specimens and field observations; it certainly must flower during part of the dry season as well, since post-anthesis collections have been made as early as March. Other post-anthesis collections have been made in April and May but especially in June. Immature fruits have been collected in February, March, May, July, October, and November, especially October. Mature fruits have been collected only in November.

Philodendron pterotum ranges from Nicaragua to Central Panama, from sea level to 1900 (mostly below 700) m elevation in *Tropical moist forest* and *Tropical wet forest* life zones. In Nicaragua it occurs only on the Atlantic slope, but in Costa Rica and Panama it occurs on both slopes.

Philodendron pterotum is a member of *P.* sect. *Philodendron* subsect. *Platypodium*. This species is characterized by its broadly ovate juvenile leaves with flattened petioles; appressed-climbing adult habit with short internodes; persistent cataphyll fibers; D-shaped petioles with slender, erect, undulate, marginal wings; and large, ovate, yellow-green-drying blades with large inflorescences with the spathe tube reddish to purplish on the outside and much darker magenta within.

No type material has survived for *P. pterotum*. The species was described from cultivated material of a juvenile plant purportedly received from the "little garden of Cl. Augustin," which the tireless traveler (Mr. Augustin) collected from Warszewicz in Venezuela. It is important to note that it was not said to have been collected in Venezuela (where it does not occur), but only that it was obtained from Warszewicz in Venezuela. There is much uncertainty involved, since the extrapolation of juvenile forms to adult plants is at best risky, even at the type locality. Given the frequency of mishaps involving the dispersal of living material among horticulturists and botanical gardens, there is always the chance of a mislabeled plant.

Still, while it is not possible to confirm the true nature of Koch and Augustin's plant, it is certain that the plant which Schott illustrated in detail (Icones #2478, #2480, #725, and #726) really does represent the plant currently being called *P. pterotum*. Although this Central American species does not occur in Venezuela, Koch and Augustin seemed not to state that the plant received from Venezuela had been collected there, only that it had been received from Warscewicz in Venezuela.

Krause (1913), in his revision of *Philodendron*, cited only a Wendland collection from Costa Rica. That collection is neither at Göttingen (GOET) nor Berlin (B) and must be lost. Since Engler reported the Wendland collection to be alive at the Berlin Botanical Garden and since Wendland made much of his material available to Schott, it might have been that it was the Wendland material from Costa Rica that Schott illustrated, rather than the Koch material received from Venezuela.

Whether these two elements corresponded to the same species is conjectural, but Schott would have conceivably had the opportunity to compare both, and it is reasonable to assume that he made the correct interpretation and that his use of *P. pterotum* for the Central American species is correct. In any event, there is a need for a neotype since no specimen actually seen by Koch, Schott, or Engler and Krause still exists. Therefore, a modern collection has been chosen here.

Philodendron pterotum may be confused with *P. fendens*, but that species differs in having blades that dry usually blackened and promptly split pinnately into segments.

Additional specimens examined. COSTA RICA. **Alajuela**: Cañas–Upala, 13.8 km N of Bijagua, 100–150 m, *Croat 36448* (MO); Llanura de San Carlos, 18–22 km N of Aguas Zarcas, 60 m, 10°31′N, 84°24′W, *Burger & Stolze 5186* (CR, F, US). **Heredia**: La Selva Field Station, *Grayum 2064* (MO); *Hammel 8150* (MO). **Puntarenas**: Golfito, 90 m, 8°39′N, 83°11′W, *Croat 67613* (MO, US); N of Palmar Norte, trail to Jalisco, 50–700 m, *Croat 35170* (MO); Palmar Norte–Panamanian border, 110 m, *Croat 79197* (CR, INB, MO); San Vito de Coto Brus–Neily, Fila de Cal and Cuesta Fila de Cal, 300–600 m, 8°41′N, 82°56.5′W, *Hammel 14161* (MO); Carara Reserve, Quebrada Bonita, ca. 35–80 m, 9°47′N, 84°36′W, *Grayum et al. 5721* (CR, MO); Isla del Caño, 40 km NW of Corcovado National Park, *Gómez 19963* (MO); Corcovado National Park, 0–39 m, 8°42′N, 83°52′W, *Janzen 11546* (MO); *11600* (MO); 0–200 m, 8°29′N, 83°36′W, *Liesner 2850* (CR, MO); 1–10 m, *Kernan & Phillips 1026* (CR, MO); Osa Península, ca. 5 km W of Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Gentry 8867* (CR, F, MO, NY); Quebrada Aguabuena–Quebrada Banegas, ca. 5 km W of Rincón de Osa, 300–400 m, 8°42′N, 83°33′W, *Grayum 4066* (CR, MO); vic. Boscosa, *Croat & Hannon 79245* (INB, MO); Río Claro, along Inter-American Highway, 30 m, *Croat 32945* (MO). **San José**: San Isidro del General–Dominical, 9 mi. SW of Río Pacuar, 680 m, *Croat 35372* (MO); Puriscal, Z.P. La Cangreja, 800 m, *Morales 2031* (CR). NICARAGUA. **Zelaya**: Siuna–Matagalpa, ca. 12.9 km before Caño Piedra del Balsamo, <200 m, *Stevens 8812* (MO); near Bil Tingnia, 6 km NW of Bonanza, 150 m, *Neill 3995* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–300 m, 13°40′N, 84°30′W, *Pipoly 4927* (MO); *4844* (MO); Cerro Waylawás, ca.

100–200 m, ca. 13°38–39′N, 84°48–49′W, *Pipoly 4201* (MO); Siuna–Empalme, Caño Calcamo, ca. 5 km al SE de Siuna, ca. 13°40′N, 84°45′W, *Grijalva & Burgos 1536* (MO); El Empalme–Limbaika, ca. 65 m, ca. 13°39′N, 84°24′W, *Stevens 12902* (MO); Cerro Livico, 7 km NE of Siuna, 500 m, *Neill 3633* (MO). PANAMA. Bahía Soldado, *Cowell 224* (NY). **Canal Area**: Gatún–Piña, ca. 3 km S of Piña, ca. 50 m, *Croat 36929* (MO); Gatún Lake, *Hutchison & Wright 2885* (BH, UC, US); Barro Colorado Island, *Elmore X20* (F, RSA); *Fairchild 3081* (US); *Croat 10903* (MO); *10265* (MO, SCZ); *7143* (MO); *6640* (MO, PMA); *6581* (MO, SCZ); *5136* (MO); *Bailey & Bailey 328* (BH); along road between Gatún Locks and Fort Sherman, ca. 3 mi. W of Gatún Locks, 1.4 mi. E of Ft. Sherman, 9°18′N, 79°38′W, *Croat 69860* (CM, MO); Summit Gardens, *Croat 10792* (MO, SCZ). **Chiriquí**: Puerto Armuelles–San Bartolo Límite, 7 mi. W of Puerto Armuelles, ca. 120 m, *Croat 35044* (MO); 1.6 m W of Puerto Armuelles, ca. 50 m, *Croat 21933* (MO). **Colón**: 4 km E of Buena Vista, Quebrada Ancha, 80 m, *Nee 7781* (MO, US); Portobelo–Nombre de Dios, 1.2 mi. beyond the junction of the road to Isla Grande, 79°35′W, 9°40′N, *Croat 49810* (MO); Santa Rita Ridge Road, 6.5 mi. E of Boyd–Roosevelt Highway, 370 m, 9°21′15″W, 79°44′W, *Croat & Zhu 76965* (MO). **Panamá**: 26.8 km E of Bayano bridge, *Folsom 3529* (MO).

Philodendron purpureoviride Engl., Bot. Jahrb. Syst. 26: 526. 1899. TYPE: Ecuador. Guayas: Balao, *Eggers 14710* (holotype, B). Figures 317–320.

Hemiepiphytic; stem appressed-climbing, scandent, often pendent, green becoming brownish to gray-green; internodes glossy, to 25 cm long, (0.8)1–2 cm diam., longer than broad, gray-green, semiglossy, ± terete, epidermis drying light yellow-brown, conspicuously fissured or ridged but smooth, frequently flaking free; roots thin, ± twisting or sinuous, few per node; cataphylls 10–29 cm long, unribbed to obtusely 1-ribbed or bluntly to sharply 2-ribbed, cream to medium green, magenta speckled, quickly deciduous, fragile; **petioles** 9–24 cm long, 8–10 mm diam., ± terete, somewhat spongy, somewhat flattened adaxially, surface semiglossy to glossy, frequently fissured, medium green, sometimes maroon-spotted; **blades** narrowly ovate-cordate, subcoriaceous, concolorous or weakly bicolorous, acuminate to long-acuminate at apex (the acumen inrolled), cordate at base, 12–23(27) cm long, 7.4–19 cm wide (1.3–1.8 times longer than wide), (0.8–2.2 times longer than petiole), broadest just below point of petiole attachment, upper surface drying yellow-green, semiglossy, lower surface glossy; anterior lobe 10–21 cm long, 7.4–19 cm wide (2.5–4.2 times longer than posterior lobes); posterior lobes (2.8)3.6–7(8.2) cm long, (3.1)4.3–7.7 cm wide; sinus hippocrepiform; midrib convex to broadly convex and slightly paler above, convex to broadly convex and paler below; basal veins ca. 3 per side, with 0–1 free to base, 2–3 coalesced to 5 mm long, flattened to raised; posterior rib 0.5–1 cm long, never naked; primary lateral veins about 3(4) per side, departing midrib at a 55–65° angle, ± straight to the margins, convex to weakly raised above, convex below; interprimary veins drying darker than surface below; tertiary veins ± obscure to visible and darker than surface below; minor veins fine below, arising from both the midrib and primary lateral veins; "cross-veins" conspicuous (in Central America). INFLORESCENCES erect, 1 per axil; peduncle (3.5)5–7(11.5) cm long, 5–7 mm diam., subterete, purplish tinged, whitish streaked; **spathe** 11–15 cm long (1.2–3(4.3–4.7) times longer than peduncle), constricted only slightly midway above the tube; spathe blade green to greenish white, with reddish speckling outside, 7–7.5 cm long, pale greenish cream inside; spathe tube violet-purple, short-lineate outside, 6.7–7 cm long, dark violet-purple inside; **spadix** sessile; ca. 13 cm long; pistillate portion white to pale greenish white, 4.5–5 cm long, 1.5 cm diam. throughout; staminate portion 8.5–9.2 cm long; fertile staminate portion white, drying reddish brown, 1.2 cm diam. throughout; sterile staminate portion 1.5 cm diam.; pistils 7.5 mm long, 1.6 mm diam.; ovary 4–5-locular, 6.2 mm long, 1.6 mm diam., with axile placentation; locules ca. 6.2 mm long; ovules 15–25 per locule, 0.2–0.25 mm long, 2–3-seriate, style similar to style type D; style apex with low style boss. INFRUCTESCENCE with pistillate spadix 6.5–7.5 cm long, 2.5–3.5 cm wide; berries 5.9 cm long, 2.5 cm diam.; seeds 24–25 per locule, yellow-orange, 1.2 mm long, 0.5 mm diam., thin and faintly striate.

Flowering in *Philodendron purpureoviride* is apparently aseasonal with post-anthesis material collected virtually year-round. Post-anthesis or early fruiting collections have been made in every month except September, but mature fruits have been collected only in January and August.

Philodendron purpureoviride ranges from Costa Rica and Panama to the Pacific slope of Colombia and Ecuador (to Los Ríos and Guayas Provinces) from sea level to 1600 m elevation in *Premontane rain forest, Tropical wet forest, Tropical wet forest* transition to *Premontane wet forest*, and *Premontane wet forest*. In Central America, it is known primarily from the Pacific slope of Costa Rica and adjacent Panama, but also from the Atlantic slope in both countries.

Philodendron purpureoviride is a member of *P.* sect. *Philodendron* subsect. *Solenosterigma*. This species is reportedly the dominant climber in west-

ern Ecuador in forests around San Sebastián, south of Jipijapa in the province of Manabí (A. Gentry, pers. comm.).

Philodendron purpureoviride is recognized by its scandent habit; stems with the epidermis drying yellow-brown, conspicuously exfoliating and frequently fissured; terete to somewhat flattened petioles about four-fifths as long as the blades; narrowly ovate-cordate blades drying yellow-green; solitary inflorescences, with the spathe tube violet-purple on both surfaces.

Philodendron purpureoviride is closest to and perhaps inseparable from *P. lechlerianum* Schott from Peru. The latter species is known from the type collected at "San Gaván" (San Gabon) in the Department of Puno, Carabaya Province, as well as a more recent collection (*D. N. Smith 6386*) from Pasco Department. *Philodendron lechlerianum* differs in having more conspicuous and prominent cross-veins. If these names prove to be synonymous, *P. lechlerianum* is older and would extend the range of the species into the Amazon basin.

Among sympatric species, *Philodendron purpureoviride* is most easily confused with *P. hederaceum*, also a vine with ovate-cordate, greenish-drying blades. The latter species is distinguished by having stems usually drying green or dark brown and without a peeling epidermis. In addition, the blades are more coriaceous, typically more broadly ovate with more (four to six) pairs of basal veins (vs. two to three pairs for *P. purpureoviride*), and generally have more prominent primary lateral veins. *Philodendron purpureoviride* may also be confused with some sterile specimens of *P. wilburii*. The latter species has much longer peduncles and stems drying darker brown and more closely fissured with the epidermis seldom exfoliating.

Central American material of *P. purpureoviride* differs from the Ecuadorian type by having conspicuous "cross-veins" throughout most of the blade. The Ecuadorian material, by contrast, has less conspicuous minor veins which lack "cross-veins" except at or near the margins. In addition, Engler's description of the inflorescence was based solely on Eggers's field label. Since the holotype is sterile and no fertile material associated with Eggers's original collection is apparently extant, further studies should investigate whether these specimens all represent the same species.

Additional specimens examined. COSTA RICA. **Alajuela**: 3.5 km W of Fortuna, 2.5 km NW of New Volcán Arenal, 1500 m, 10°28′N, 84°41′W, *Taylor & Taylor 11706* (MO, NY, US); Cañas–Upala, 4 km NNE of Bijagua, 400 m, *Croat 36267* (MO); Upala, 600 m, *Rivera 1559* (INB, MO). **Cartago**: 12 km S of Turrialba by air, 4 km SE of Pejibaye along Río Gato, 700 m, 9°48′N, 83°42′W, *Liesner 14355* (CR, MO); Río Reventazón, Turrialba, 500–600 m, 9°53.5′N, 83°38.5′W, *Grayum & Schatz 5242* (CR, MO); Tucurrique, Las Vueltas, 635–700 m, *Tonduz 13312* (US). **Limón**: Turrialba–Limón, along Highway 32, ca. 11 mi. S of Siquirres, 650 m, *Croat 43332* (MO); Río Telire, Bajo Telire, 400–600 m, *Gómez 24119* (MO). **Puntarenas**: Zona Protectora Las Tablas, Parque International La Amistad, Finca Cafrosa, 1600–1800 m, 8°53′20″N, 82°50′30″W, *Mora 139* (CR, MO); 1680 m, *Alfaro & Navarro 29* (INB); Cerro Anguciana, 950–1150 m, 8°49′18″N, 83°11′15″W, *Grayum 10647* (CR, MO); Palmar Norte to Jalisco, 780–960 m, 8°59.5′N, 83°28′W, *Grayum 9141* (CR, F, K, MO, US); 50–700 m, *Croat 35203* (MO); Las Cruces–Neily, Fila de Cal, 1000–1400 m, *Gómez 19635* (MO, US); Cantón Golfito, 100–500 m, *Morales et al. 1903* (CR, INB); 9 km W of La Palma, along Río Rincón, *Grant & Rundell 92-02203* (CR, MO); Golfo Dulce area, Cantón de Osa, vic. of Esquinas Experiment Station, 0 m, *Allen 5370* (MO, UC, US); W of Rincón de Osa, 250–540 m, 8°42′N, 83°31′W, *Croat & Grayum 59857* (CAS, CM, CR, MO, NY); Villa Briceño–Golfito, Fila Gamba, ca. 6 km from Golfito airport, <100 m, 8°41′30″N, 83°12′W, *Croat 59902* (CR, MO); Parque Nacional Corcovado, Dos Brazos de Rio Tigre, Jiménez, along Río Madrigal, 600 m, 8°29′50″N, 83°28′55″W, *G. Herrera 4728* (CR, MO). **San José**: San Isidro del General–Dominical, 9 mi. SW of Río Pacuar, 680 m, *Croat 35348* (MO); Carara Reserve, W Montañas Jamaica, ca. 3 km NE of Bijagual de Turrubares, 500–600 m, 9°45′30″N, 84°33′W, *Grayum et al. 5851* (CR, F, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, near road to Chiriquí Grande, 650 m, 8°45′N, 82°15′W, *McPherson 9925* (MO). **Chiriquí**: Burica Peninsula, 11 mi. W of Puerto Armuelles, vic. of San Bartolo Límite, 100–500 m, *Liesner 84* (F, MO, US); 450 m, *Busey 595* (F, MO); "Ojo de Agua," Finca Hartmann, vicinity of Santa Clara (between Volcán and Río Sereno), 1520–1750 m, 8°50′N, 82°45′W, *Croat 66290* (MO, PMA, US); ca. 13 km from Río Sereno, *McPherson & Richardson 15968* (B, K, MEXU, MO, PMA, US). **Coclé**: El Valle region, La Mesa, above El Valle de Antón, 860–900 m, *Croat 37421* (MO); Finca Macarenita, 800 m, 8°36′N, 80°07′W, *Croat & Zhu 76677* (MO). **Darién**: Cerro Pirre region, Cana, 500–600 m, *Croat 37631* (MO); W slope along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77117* (MO). **Veraguas**: Santa Fe area, between Santa Fe and Calovébora, 1.7 mi. past Alto Piedra School, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76865* (MO).

Philodendron purulhense Croat, sp. nov. TYPE: Guatemala. Alta Verapaz: El Progreso–Cobán, on Hwy. CA-14, 2–3 mi. S of Purulhá, 1500–1720 m, 15°13′S, 90°12′W, 21 July 1977, *Croat 41752* (holotype, MO–2582045; isotype, GUAT). Figures 321–323, 325, 326.

Planta hemiepiphytica aut raro terrestris; internodia brevia, usque 6 cm diam.; cataphylla 20–30 cm longa, 2-costata, acute D-formata, persistentia semi-intacta; petiolus subteres, aliquantum spongeosus, obtuse complanatus adaxialiter, 32–52 cm longus, 1.5–2 cm diam.; lamina ovata vel ovato-cordata, 25–48 cm longa, 18.5–40 cm lata, in sicco atribrunnea vel nigrescens; nervis basalibus liberis ad basim; inflorescentia 1; pedunculus 2.5–7 cm longus; spatha 10–17 cm longa; lamina spathae extus vir-

idi, breve lineata; intus viridi; pistilla 6–7-locularia; loculi 13–20-ovulati.

Hemiepiphytic or rarely terrestrial, growing 3–6 m high in trees; stem appressed-climbing or creeping; internodes short, semiglossy, to 6 cm diam., broader than long, dark green, epidermis intact; roots moderately dense, drying dark brown, ca. 3 mm diam.; cataphylls 20–30 cm long, 2-ribbed, sharply D-shaped, persisting semi-intact with brownish fibers at upper nodes; **petioles** 32–52 cm long, 1.5–2 cm diam., subterete, somewhat spongy, obtusely flattened adaxially, surface semiglossy, short-lineate, usually drying brown to blackened; **blades** ovate to ovate-cordate, subcoriaceous, slightly bicolorous, acute to acuminate at apex, cordate at base, 25–48 cm long, 18.5–40 cm wide (1.2–1.97 times longer than wide), (0.6–0.98 times the petiole length), about equal in length to petiole, upper surface somewhat silvery, semiglossy, lower surface drying dark brown to blackish; anterior lobe 20–38 cm long, 18.7–38 cm wide (2.1–3.1(3.6) times longer than posterior lobes); posterior lobes rounded, 7–17 cm long, 8–17 cm wide; sinus usually hippocrepiform, 12 cm deep; midrib flat, slightly paler than surface above, convex, paler than surface below; basal veins 4–7(8) per side, with all free to base, third and higher order veins coalesced 1.5–4 cm long; posterior rib naked for 1.5 cm; primary lateral veins 3–6 per side, departing midrib at a 35–40° angle, ± straight to the margins, sunken above, convex and paler than surface below; minor veins moderately distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES 1 per axil; peduncle 2.5–7 cm long, 8–10 mm diam., whitish streaked; **spathe** 10–17 cm long (2.4–3.4(4) times longer than peduncle), constricted slightly above the tube, ± ellipsoid; spathe green, short-lineate outside, reddish purple throughout inside; spathe tube 5 cm long; **spadix** sessile; 10–13 cm long; pistillate portion 4–4.5 cm long, 1.7–2.3 cm diam. at base, 2–2.7 cm diam. midway, 1.7–1.9 cm diam. near apex; staminate portion 8–8.5 cm long; fertile staminate portion 1.8–2 cm diam., sterile staminate portion usually much broader than pistillate portion at anthesis, weakly tapered toward apex, scarcely or not at all constricted above the sterile portion, 1.4–1.8 cm diam. midway, 11–12 mm diam. 1 cm from apex, bluntly acute at apex; sterile staminate portion not very obvious, ca. 1.3 cm long, abruptly contracted at base, as broad as or narrower than the pistillate portion; pistils 6.2 mm long, 3.4 mm diam.; ovary 6–7-locular, 5 mm long, 3 mm diam., with axile placentation; locules 5 mm long, 1 mm diam.; ovules 13–20 per locule, somewhat transparent, 1 mm long, much longer than funicle; funicle 0.2 mm long, adnate to lower part of partition, style 1 mm long, 3 mm diam., similar to style type D; style apex ± rounded; style boss broad, pronounced; stigma 1–1.1 mm diam.; the androecium truncate, oblong, prismatic, margins irregularly 4–5-sided, 1 mm long, 2–2.5 mm diam. at apex. INFRUCTESCENCE with pistillate spadix 4.5–5 cm long, 3–4 cm diam.; berries 1 cm long, 4 mm diam.; seeds 6–8 per locule, oblong-ellipsoid, 2.2–2.5 mm long, 0.7–0.9 mm diam., sticky.

The flowering phenology in *Philodendron purulhense* is poorly known. No flowering collections have been made, and only one post-anthesis collection is known (July), but immature fruiting collections are known from March, July, September, October, and November. This might suggest that the species flowers throughout at least a substantial part of the rainy season and perhaps also in the dry season (December through April).

Philodendron purulhense ranges from southern Mexico (Chiapas) to Guatemala (Alta Verapaz) and Honduras (Cortés and Olancho), at 1360 to 1870 m elevation in *Tropical Lower Montane wet forest* and *Premontane wet forest* life zones.

Philodendron purulhense is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is characterized by its short internodes; sharply D-shaped to two-ribbed cataphylls persisting semi-intact; subterete petioles (about as long as the blades), dark brown to blackish-drying; ovate-cordate blades with basal veins free or weakly coalesced and scarcely or not at all naked on the usually hippocrepiform sinus; solitary, short-pedunculate inflorescence, more or less elliptic green spathe; and ovaries with 13–20 ovules per locule.

Philodendron purulhense may be confused with *P. advena* because leaves of the latter species dry a similar color. *Philodendron advena* differs in having long internodes, deciduous cataphylls, more or less sagittate blades, and one to three (four) ovules per locule.

Additional specimens examined. GUATEMALA. **Alta Verapaz**: Tactic, Río Frío, 1400–1500 m, *Standley 90510* (F); Tactic–Tamahú, 1500–1600 m, *Standley 90820* (F); Río Carchá, Cobán–San Pedro Carchá, ca. 1360 m, *Standley 89902* (F). **Baja Verapaz**: Highway CA-14 to Cobán, *Croat 41189* (MO); Biotopo del Quetzal, WNW of Purulhá, 1500–1600 m, *Stevens et al. 25446* (MO); Mpio. Purulhá, El Progreso–Cobán, 1620–1720 m, 15°13′N, 90°12′W, *Croat & Hannon 63765* (CAS, CM, K, L, MEXU, MO, US, USCG). HONDURAS. **Cortés**: Parque Nacional Cusuco, Río de Cusuco, ca. 22 km W of San Pedro Sula, 1500 m, 15°30′N, 88°13′W, *Evans 1490* (EAP, MO). **Ocotepeque**: Cordillera de Celaque, 3 mi. N of Belén Gualcho,

1870 m, 14°30′06″N, 88°48′02″W, *Davidse et al. 35340* (MO). MEXICO. **Chiapas**: Mpio. Jitotol, 5 km SE of Jitotol, along road to Bochil, 1600 m, *Breedlove & Davidse 55077* (MO); Mpio. La Trinitaria, 4 km E of Laguna, near Dos Lagos, 1300 m, *Breedlove 38810* (CAS); Mpio. Las Margaritas, 12 km E of Tziscao, 1200–1300 m, *Davidse et al. 29865* (MO).

Philodendron radiatum Schott, Oesterr. Bot. Wochenbl. 3: 378. 1853. TYPE: Mexico (holotype lost). Schott ic. 2623 (neotype, here designated). Figures 1, 324, 331–335.

Epiphytic or hemiepiphytic, rarely terrestrial; stem appressed-climbing, creeping if terrestrial, sap clear to orange, watery, sticky, leaf scars conspicuous, 2–4(7.5) cm long, 2.5–6(7) cm wide; internodes thick, 3–7(12) cm long, (1)3–8 cm diam., about as long as broad or longer than broad, dark green to gray-green, sometimes scurfy and light brownish tan, transverally lined (raised 2 mm); roots 4 mm diam., with swollen nodes and branched tips; cataphylls to 38 cm long, soft, bluntly to sharply 2-ribbed, rarely unribbed, green, sometimes conspicuously reddish-lineate, deciduous; **petioles** 28–108 cm long, (2–3)4–17 mm diam., terete or subterete to obtusely flattened adaxially, dark green, surface dark greenish or to greenish red-lineate; sheath persisting, sometimes moderately spongy; **blades** ± triangular-ovate in outline, (15)27–101 cm long, (11)25–90 cm wide (ca. 0.8–2.1 times longer than wide), (0.5–1.7 times longer than petiole), broadest at point of petiole attachment, thinly coriaceous, weakly to moderately bicolorous, semiglossy, acuminate to long-acuminate at apex, upper surface dark green, lower surface slightly paler, usually drying yellow-brown to reddish brown on both surfaces; margins weakly incised-lobate to usually deeply incised-lobate to within 1–8 cm of midrib, rarely entire and sagittate; apex often acute, sometimes acuminate, very short acuminate or ± rounded (the acumen tightly inrolled if present, 1–8 mm long), lobed-cordate at base; basal segments pinnatifid, lateral segments entire, sinuate or the lowermost of the anterior lobe pinnately lobed with 1–2 lobes on each side, final divisions linear-lanceolate in shape (0.9–2.1 times longer than wide), segment apex obtuse to broadly obtuse; interlobal sinuses 0.7–0.97 the length of the lobes; basal sinus hippocrepiform to obovate or closed, 3–15 cm deep; midrib slightly raised to convex, weakly reddish green-lineate, concolorous to paler than surface above, convex to prominently raised to round-raised below; basal veins 4–5(8) per side, directed into the segments of the posterior lobe, 0–1 free to base, (1)2–4 coalesced to 3 cm long, naked 1–6 cm; posterior rib absent; primary lateral veins 3–8 per side, departing midrib at a 50–60° angle, straight to margin, weakly raised above, raised to convex and paler than surface below; minor veins moderately visible, paler and slightly raised below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1–3(4) per axil; peduncle 2–12 cm long, (3)5–10(19) mm diam.; **spathe** erect, 11–25 cm long (1.3–6.3 times longer than peduncle), obscurely striate, margins paler; spathe blade cuspidate at apex, pale green to yellowish green, semiglossy, sparsely purplish-dotted outside, pink to dull red or pale brownish (post-anthesis) inside; spathe tube dark purple-violet or dark green, sometimes tinged purple-violet outside, 4 cm diam., dark purple-violet inside; **spadix** sessile to weakly stipitate, cylindrical to weakly tapered; staminate portion creamy white, protruding forward at anthesis, pointed at apex, 10–17 cm long; pistillate portion whitish, weakly obovoid, 3.5–5.2 cm long (1 cm shorter on back side), 1.1–1.8 mm diam. at apex, 1.5–1.9 mm diam. at middle, (7)17 mm wide at base; staminate portion 6.3–8.1 cm long; fertile staminate portion tapered, 1–1.9 cm diam. at base, 1.2–1.6 cm diam. at middle, 0.9–1.4 cm diam. ca. 1 cm from apex, broadest at the base, slightly constricted above the base; sterile staminate portion as or slightly broader than the pistillate portion, white with tan ring around apex, 0.7–2 cm diam.; pistils (1.6)4–5(8) mm long, (1)2.8–3.2(5.2) mm diam.; ovary (7)8-locular, (1.6)3.3–4(6.7) mm long, 1.5–3(5.2) mm diam., with axile or sub-basal placentation; locules (0.6)1.9–3.4(6.5) mm long, 0.5–0.8(1) mm diam.; ovule sac 1.8(3.5) mm long; ovules 8 per locule, 1–2-seriate, contained within translucent, gelatinous ovule sac, 0.1–0.3 mm long, longer than funicle; funicle 0.1–0.2 mm long, style 0.3–0.5 mm long, 1.2–3 mm diam., similar to style type B (rarely C); style apex flat to weakly rounded, sometimes domed; stigma usually hemispheroid, sometimes subdiscoid, pink, 1.2–1.5 mm diam., 0.6–0.7 mm high, covering entire style apex; the androecium truncate, oblong, prismatic, margins irregularly 3–5-sided, sometimes weakly scalloped, 1 mm long, (0.7)2.5–2.7 mm diam. at apex; thecae cylindrical, 0.3 mm wide, ± parallel to one another and contiguous; sterile staminate flowers usually truncate, sometimes clavate or irregularly 5–6-sided, 1.1–2.9 mm long, 0.6–1.8 mm wide. INFRUCTESCENCE 11–17 cm long, 4.5 cm diam.; pistillate spadix 6–8 cm long, 2.5–3.5 cm diam.; berries white, somewhat translucent, 4 per locule, oblong, sticky.

Philodendron radiatum ranges from Mexico (San Luis Potosí to Chiapas and on both Atlantic and Pacific slopes in Chiapas) to Colombia (Antioquia), from sea level to usually no more than 700 m (rare-

ly 1250 to 1860 m; most collections are from below 100 m) elevation. It is perhaps more widespread in South America than collections indicate (only two are known). The plants are very large and difficult to collect and may have been overlooked in other areas.

This species is highly variable morphologically and ecologically versatile as well. In Mexico, it occurs in "Selva Alta Perennifolia," "Selva Mediana," and "Selva Baja Caducifolia" in mesic areas on the Atlantic slope as well as in "Selva Mediana Subperennifolia" and "Selva Baja Subperennifolia" in the drier Yucatán Peninsula. On the Pacific slope it also occurs in areas of "Bosque Pino-Encino." In Central America, this taxon occurs principally in *Tropical moist forest* but also in *Premontane wet forest* and drier parts of *Tropical wet forest.*

Philodendron radiatum is a member of *P.* sect. *Polytomium. Philodendron radiatum* has two varieties, the typical variety having more deeply divided leaf blades with the segments often incised almost to the midrib and variety *pseudoradiatum* with the blades only weakly incised-lobate (less than half the distance to the midrib). While the latter variety is restricted to southwestern Chiapas, even populations of the typical variety on the western slope of Central America have less deeply incised-lobate blades than those on the Atlantic slope. There is also considerable clinal variation in the width of the divisions throughout Central America, with plants in Mexico having, on average, broader pinnae (averaging 4.5 cm wide) than those in Panama, for example, where the pinnae average only about 3 cm wide. Leaves of Mexican populations of *P. radiatum* also consistently lack free basal veins, whereas elsewhere in Central America such veins are present. In western Mexico and Guatemala, plants are also more likely to have longer internodes and to occur more frequently on rocks or creeping over the ground than plants on the more mesic Atlantic slope of Central America.

KEY TO THE VARIETIES OF *P. RADIATUM*

1a. Blades deeply lobed, the divisions near the middle of the blade extending more than ¾ the way to the midrib ..... var. *radiatum*

1b. Blades shallowly lobed, the divisions near the middle of the blade extending less than ½ the way to the midrib ..... var. *pseudoradiatum* (Matuda) Croat

Philodendron radiatum Schott var. **radiatum**

Philodendron augustinum K. Koch, in A. Braun et al., Append. sp. Hort. berol. 1853: 4. 1853–1854. TYPE: Central America. Without exact locality (holotype, B? lost). Schott ic. 2605 (neotype, here designated).

Philodendron polytomum Schott, Bonplandia 7: 164. 1859. TYPE: Mexico. Veracruz: Colipa, Hac. de Sta. Bárbara, *Liebmann s.n.* (holotype, C; isotype, K not seen).

Philodendron impolitum Schott, Prodr. Syst. Aroid. 291. 1860. TYPE: Costa Rica, *Wendland s.n.* (not seen).

Internodes 3–7 cm long, 3–8 cm diam.; cataphylls bluntly to sharply 2-ribbed; **petioles** 33–108 cm long; blades deeply lobed, the divisions near the middle of the blade extending more than ¾ the way to the midrib, 21–101 cm long, 25–90 cm wide; posterior lobes (8)12.5–25 cm long, (9)16–18 cm wide; primary lateral veins 3–8 cm long; basal veins 4(5) per side, (1)2–4 coalesced to 3 cm long, naked 1–6 cm. INFLORESCENCES 1–3(4) per axil; **spathe** 11–25 cm long; **spadix** 10–13 cm long; pistillate portion 3.5–5.2 cm long; pistils (3)4–5(8) mm long; ovaries with axile placentation; style similar to style type B (rarely C).

Flowering in *Philodendron radiatum* var. *radiatum* is documented by few flowering collections made in February, August, and September. Postanthesis collections are common, from every month of the year, and there are no clearly marked differences in the phenology of this species in different parts of Central America. Material was seen at various stages of development from all parts of Central America in about equal numbers. Mature fruits are known only from February and May.

Philodendron radiatum var. *radiatum* is characterized by its moderately thick, mostly short internodes; sharply two-ribbed, deciduous cataphylls; terete petioles; and especially by its deeply incised-lobate leaf blades that mostly linear to linear-lanceolate segments, themselves often lobate toward the base of the blades.

Philodendron radiatum var. *radiatum* might be confused with *P. dressleri* and *P. warszewiczii*, Central American species with incised-lobate leaf blades. *Philodendron dressleri* differs in having thicker leaf blades, more succulent stems with shorter internodes, and especially by having blades that are incised lobate only about midway to the midrib. In addition, *P. dressleri* has one inflorescence per axil and 3–4 locules per ovary, while *P. radiatum* has 1–3(4) inflorescences per axil and 7–8 locules per ovary. *Philodendron warszewiczii* differs by having thinner blades, drying papyraceous with the minor veins distinctly visible. In addition, the lateral leaf blade segments usually have three or more lobes per side. *Philodendron radiatum*, in contrast, has blades drying subcoriaceous with the minor veins rather indistinct and with the

lateral leaf blade segments usually 1–2-lobed per side.

Philodendron radiatum var. *radiatum* has a unique attractant, whose odor profile is made up almost entirely of compounds unique to it, and is pollinated by a new species of *Cyclocephala* (Schatz, 1990).

Additional specimens examined for P. *var.* radiatum. BELIZE. Honey Camp, *Lundell s.n.* (US); Maskall, *Gentle 1141* (MICH, NY); Gracie Rock, 1.5–4 mi. S of Mile 22 on Western Highway, 100 m, *Liesner & Dwyer 1460* (MO); Crooked Tree Village, 60 m, 17°47′N, 88°32′W, *Davidse & Brant 33146* (MO). **Cayo**: Roaring Creek, *Dwyer 12677* (MO); 1.5 mi. W of Augustine, Río Frío, ca. 450 m, *Sutton et al. 211* (BM); Hummingbird Highway, Mile 20, *Dwyer & Liesner 12130* (MO); Chiquibul National Park, Caracol Archaeological Reserve, 550 m, 16°45′N, 89°07′W, *Ingram & Ferrell-Ingram 1935* (MO); Río Ma Cal, San Luis–Cuevas, 1050 ft., *Croat 23534* (MO); Vaca, *Gentle 2552* (MICH). **Corozal**: edge of New River, Pueblo Nuevo, *Gentle 473* (CM, MICH); Cerro Maya Ruins, Lowry's Bright, *Crane 348* (LL); *Gentle 617* (MICH). **Orange Walk**: road to Trinidad, ca. 5 km N of August Pine Ridge, 100 m, 18°N, 88°42′W, 100 m, *Davidse & Brant 32791* (MO); Pulltrouser Swamp, *Lincoln 20* (MO). **Toledo**: Punta Gorda highway, 1 mi. E of junction to San Antonio, ca. 100 ft., *Croat 24512* (MO); Solomon Camp, vic. of Richardson Creek and Bladen Branch junction, Maya Mountains foothills, 80–420 m, 16°32–33′N, 88°45–46′W, *Davidse & Brant 32198* (MO); Columbia Forest Station Area, 1.5 mi. S of Mayan Village of San José, *Croat 24335* (MO); *Holst 4303* (MO). COSTA RICA. **Alajuela**: Cañas–Upala, 10 km N of Bijagua, 200 m, *Croat 36488* (MO). **Heredia**: La Selva Field Station, *Grayum 2534A* (DUKE); 100 m, *3022* (DUKE); *Jacobs 2290* (DUKE); *2707* (MO); 10°26′N, 84°W, *Burger & Stolze 5921* (BM, CR, US); 100 m, 10°26′N, 84°01′W, *Gentry & Ortiz 78615* (MO); Río Sucio, near Puerto Viejo, 20 m, *Croat 35680* (MO); Puerto Viejo–Guápiles, 7 km N of Buenos Aires, 10°23′30″N, 83°48′30″W, *Croat 68386* (MO); Río Sarapiquí, S of La Virgen, 200 m, *Lent 33* (MO); La Tirimbina, 220 m, *Hunter 821* (WIS). **Limón**: Barra del Colorado, N side, 0–2 m, 10°47′N, 83°35′W, *Stevens 24133* (CR, MO); Barra del Colorado–Río San Juan, Laguna de Atrás, 5 m, 10°48-52′N, 83°38′W, *Davidse & Herrera 31512* (CR, MO); Cerro Coronel, E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 23845* (CR, MO); Parque Nacional Tortuguero, Estación Agua Fría, 2 m, *Robles 1398* (CR, MO); 40 m, 10°26′N, 83°35′W, *1730* (CR, MO); 600 m S, 4 m, 10°32′N, 83°30′W, *1846* (CR, MO); Cahuita, *Poveda 1166* (CR, MO); Cahuita–Limón, 0–10 m, 9°44′N, 83°20′W, *Baker & Burger 157* (CR, NY); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8729* (MO, RSA); *8437* (RSA); Río Colorado, 3.5 airline km S of Islas Buena Vista, 10–120 m, 10°39′N, 83°40′40″W, *Davidse & Herrera 31268* (MO); Barra del Colorado, 1–5 m, 10°47′40″N, 83°25′30″W, *Davidse & Herrera 30882* (MO); Río Pacuare, 50–100 m, 10°15′N, 83°29′W, *Burger & Liesner 6894* (MO); 7 km SE of Bribrí, 100–250 m, *Gomez 20315* (MO); 1 mi. SW of Bribrí, <50 m, *Croat 43228* (CR, MO); vic. of Moin, 0 m, 10°N, 83°04′W, *Croat 61207* (MO); Bahía de Portete Parque Nacional, 0–10 m, 10°N, 83°05′W, *Thompson & Rawlins 1175* (CM); Río Reventazón, Finca Montecristo, below Cairo, 25 m, *Standley & Valerio 48969* (US). EL SALVADOR. La Cebadilla, *Calderón 1245* (US). **San Salvador**: Tonacatepeque vicinity, *Standley 19538* (GH, NY, US); *Calderón 201* (GH, NY, US). GUATEMALA. **Alta Verapaz**: *Tuerckheim 8330* (US); eastern portions of Verapaz and Chiquimula, *Watson 194* (GH); near Finca Sepacuite, *Cook & Griggs 724* (US); Cubilquitz, 350 m, *Tuerckheim 8330* (US); Guatemala–El Estor, 5 mi. W of Tucurú, 600 m, *Croat 41509* (MO); Tucurú–El Estor, Finca Argentina, above Papalha, 15 mi. W of Telemán, 550–650 m, *Croat 41550* (MO); ca. 6 km NE of Panzós, 500 m, *Croat 41616* (MO). **Izabal**: Quiriguá vicinity, 75–225 m, *Standley 23939* (US); ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41803* (MO); Río Frío, Cerro San Gil, 75–150 m, *Steyermark 41534* (MO, NY); W of El Estor and abandoned nickel mine, 1–10 m, *Stevens & Martínez 25283* (MO). **Petén**: La Libertad, *Lundell 2645* (MICH, NY); El Paso, *Lundell 1571* (MICH); Uaxactun, *Bartlett 12702* (MICH); Tikal National Park, *Contreras 105* (LL). **Quezaltenango**: along CA-2, 4 mi. NW of turnoff to Coloba, *Croat 32767* (MO); Coatepeque–Retalhuleu, Hwy. CA-2, 3 mi. S of turnoff to Colomba, 600 m, *Croat & Hannon 63414* (MO, US). **Sacatepéquez**: Volcán Santa Clara, 1250–2650 m, *Steyermark 46621* (MO). HONDURAS. Puerte Sierra, *Wilson 321* (NY). **Atlántida**: Lancetilla Valley, near Tela, *Standley 52945* (US); *53668* (US); *53985* (US); ca. 10 mi. SE of Tela, Río Lancetilla, 10–150 m, *Croat 42631* (MO); Río Cangrejal, 5 km inland from La Ceiba, *Blackmore & Chorley 4155* (BM, MO, UNAH); Río Sambo, Tocoa–La Cieba, 11.3 mi. from Río Cangreja Bridge at La Ceiba, 30 m, 15°47′N, 86°30′W, *Croat & Hannon 64581* (BM, MO); Parque Nacional Pico Bonito, ca. 10 km SW of La Ceiba, 160 m, 15°42′N, 86°51′W, *Evans 1675* (MO). **Colón**: Río Negro, Trujillo, *Clewell et al. 4345* (MO). **Copán**: ca. 4 mi. E of Copán, 800 m, *Croat 42502* (MO); 10 mi. W of Copán, road to La Entrada, 700 m, *Croat 42516* (MO). **Cortés**: Lago Yojoa, Punta del Cacao, 650 m, 14°05′30″N, 87°58′W, *MacDougal et al. 3079* (MO); Ocote Arrancado, 50 km N Lago de Yojoa, *Nelson et al. 5868* (MO, VBD); Puerto Cortes–Guatemalan border, 2–3 mi. SW of Omoa, *Croat 42558* (MO); N of Lago de Yojoa, along old Highway 1, ca. 2–6 mi. from junction with new Highway 1, SW of Santa Cruz de Yojoa, 600 m, *Croat 42745* (MO). **Gracias a Díos**: Río Plátano Biosphere Reserve, Las Marías (Batil Tuk), 30 m, *Knees et al. 2825* (BM). **Morazán**: El Zamorano, 800 m, *Molina 34353* (MO). **Olancho**: El Jocomido–Cerro El Mulato, *Blackmore & Heath 1686* (BM, MO); Gualaco–San Esteban, Río Olancho, 7.4 mi. NE of San Esteban, 540 m, 15°20′N, 85°42′W, *Croat 64365* (K, MO, NY). **Santa Bárbara**: Lago Yojoa, Punta Gorda, 650 m, 14°52′N, 88°W, *MacDougal et al. 3126* (MEXU, MO, NY); 630 m, 14°53′N, 88°W, *Liesner 26769* (MO); 700 m, *Croat 42752* (MO); El Novillo, 640 m, 14°53′N, 88°00′30″W, *Evans 1044* (MO). **Yoro**: Aguán River Valley, Coyoles, *Yuncker et al. 8624* (GH, MO, NY, UC, US). MEXICO. Location unspecified, Reko 3690 (US); *Sandoval 14* (US). **Campeche**: Mpio. Hopechén, Rancho El Carmen, 33–35 km S of Xmaben on road from Hopelchén to Xpujil, near Xpanzil, 200 m, 18°58′N, 89°20′W, *Sanders et al. 9735* (MO); Huatusco, *Sandaval 14* (US); Patria, *Engler 197* (BM, GH); Santa Leonor, E of Río San Pedro, *Barlow 16/8* (BH). **Chiapas**: San Manuel, ca. 15 km above Palenque, on road to Ocosingo, ca. 500 m, *Madison 7312* (SEL); Escuintla–El Triunfo, 1 mi. N of Escuintla, 100 m, *Croat 43811* (MEXU, MO); Esperanza–Escuintla, *Matuda 16662* (F, MEXU); *17788* (NY); 150 m, *18045* (MEXU);

Tapachula–Nueva Alemán, 4 mi. N of Tapachula, 250 m, *Croat 43794* (MO); Escuintla–El Triunfo, ca. 8.5 mi. NE of Escuintla, 250 m, *Croat 43820* (MO); Escuintla–Monte Ovando, 2.8 km NW of Turquiz, ca. 100 m, *Croat 47511* (MO); Acacoyagua, Cerro Ovando, 800–900 m, *Croat 78548* (CHIP, MO); Huixtla–Motozintla de Mendoza, 4.8 km N of Huixtla, ca. 200 m, *Croat 47523* (MO); 2 mi. S of Chiapas border, along Hwy. 195, 8 mi. N of Pichucalco, 80 m, *Croat 40088* (MO); 5 mi. SE of Palenque, on road to Ocosingo, 200 m, *Croat 40135* (MO); Palenque–Bonampak, 89–90 mi. SW of Palenque, 350–370 m, *Croat 40217* (MO); 73 mi. SE of Palenque, 460 m, *Croat 40267* (MO); Ocozocoautla–Apitpac, 20 mi. N of Ocozocoautla, 700 m, *Croat 40650* (MO); 5 mi. N of Ocozocoautla, 1000 m, *Croat 40543* (MO); Motozintla de Mendoza–Huixtla, 15 mi. S of Motozintla de Mendoza, 900 m, *Croat 40765* (MO); Mpio. Ixtacomitan, 7 km SW of Ixtacomitan, 250 m, *Breedlove 45915* (MO); Mpio. Mapastepec, Sierra de Soconusco, new unfinished road to Tuxtla Gutiérrez, 200 m, 15°31′N, 92°50′W, *Croat 63382* (B, K, MO, NY, US); Mpio. Ocosingo, Lacanja–Chanzayab, Palenque–Boca Lacantum, 340 m, *Martínez 15071* (MO); Laguna Ocotalito, 12 km N of Monte Líbano, trail to Chancala, 980 m, *Martínez 17029* (MO); Bonampak, 520 m, *Breedlove & Almeda 58051* (MO); Mpio. Palenque, 8–9 km S of Palenque, 300 m, *Breedlove & Strother 46895* (CAS); 25 km S of Palenque, 300 m, *Breedlove & Almeda 57318* (CAS); Mpio. Tzimol, 15 km S of Comitán, 1200 m, *Breedlove 53732* (CAS). **Oaxaca**: *Williams 9173* (US); 14 mi. S of Tuxtepec, *Moore & Bunting 8904* (BH, MO); *8910* (BH); Tuxtepec–Oaxaca, 0.5 mi. S of Valle Nacional, Highway 175, 120 m, *Croat 39700* (MO); 3 km S of Hidroeléctrica Temascal, 50 m, *Cortés et al. 875* (MO); Uxpanapa region, Esmeralda–Río Verde, 1.1 mi. S of Esmeralda, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63234* (MO); Jalpan, 2–3 km E of La Baquilla, Río Santa María, 270–320 m, *Carranza & Zamudio 4548* (MO); ca. 1.5 km E of La Boquilla, 270–320 m, *Carranza & Díaz 4721* (MO). **San Luis Potosí**: Highway 85, 6 mi. NW of Tamazunchale, 250 m, *Croat 39262* (MO); Tamazunchale, *Edwards 626* (DS, MO). **Tabasco**: 30 mi. E of Minatitlán, *Barkley & Carr 36221* (GH); Alemán, 10 mi. NW of Cardenas, *Barlow 26/25* (BH); Mpio. Cárdenas, vic. Cárdenas, *Cowan 2021* (MO); Mpio. Huimanguillo, km 12.6 de la desviación de Huimanguillo, *Cowan & Magaña 3255* (CAS, NY). **Veracruz**: Huatusco–Puente Nacional, El Mirador, 21 km E of Huatusco, ca. 1200 m, *Croat 43974* (MO); *Moore & Bunting 8855* (BH); Playa Escondida, N of Sontecomapan, along Caribbean cliffs, 10–60 m, *Gentry et al. 32610* (MO); Córdoba–Veracruz, San José de Gracia, ca. 750 m, *Croat 39612* (MO); Highway 180, 6 mi. E of Coatzacoalcos, *Croat 40064* (MO); NW of Misantla, 2.4 mi. on road to Martínez de la Torre, ca. 320 m, *Moore & Bunting 8946* (BH); Dtto. Papantla, *Kelly 126* (BH); Mpio. Coatepec, 5 km by air SE of Tuzamapan, 680 m, 19°21′N, 96°50′W, *Nee & Taylor 26026* (NY); Mpio. Cosamaloapan, 10 km by air NW of Tres Valles, 25 m, 18°17′N, 96°13′W, *Nee & Taylor 29306* (NY); Mpio. Hidalgotitlán, 1 km SE of Agustín Melgar, 100 m, 17°15′N, 94°33′W, *Nee 29765* (NY); Mpio. Naolinco, 2 km from Concha al Espinal, 900 m, *Ortega 630* (MO). **Yucatán**: Izamal, 20°56′N, 89°01′W, *Gaumer 23200* (GH, NY, US); *1413* (GH, MO); Uayma, *Schott 766* (BM). NICARAGUA. **Boaco**: Boaco–Camoapa, N slope of Cerro Mombachito, 500–900 m, ca. 12°24–25′N, 85°32–33′W, *Stevens & Grijalva 14699* (MO); Hwy. 33, vic. Río Quilan bridge, ca. 300–310 m, 12°35′N, 85°32′W, *Stevens 9330* (BM, MO). **Chontales**: Juigalpa–La Libertad, ca. 17.4 km NE of Río Mayales, at ford of Río El Bizcocho, 350–400 m, ca. 12°12′N, 85°17′W, *Stevens 4093* (BM, MO); *4095* (BM, MO); ca. 2.8 km above Cuapa, 400–500 m, ca. 12°17′N, 85°23′W, *Stevens 3671* (MO, PMA). **Estelí**: km 167 on Hwy. 1, ca. 15.8 km N of entrance to Estelí, 825–850 m, ca. 13°15′N, 86°22′W, *Stevens 5788* (MO). **Jinotega**: Río Bocay, Salto Acatulu, ca. 130 m, 14°13′N, 85°10′W, *Stevens et al. 16749* (MO). **Madriz**: Cerro Quisuca, 1100–1250 m, ca. 13°30′N, 86°31′W, *Stevens & Grijalva 16063* (MBM, MO). **Managua**: Ciudad Managua, Reparto Bolonia, *Guzmán et al. 1071* (MO). **Nueva Segovia**: Río San Fernando Valley, ca. 5.2 km N of San Fernando, 13°2–3′N, 86°19–20′W, *Stevens 3245* (BM, MO). **Río San Juan**: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23427* (MO); Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill & Vincelli 3620* (MO). **Zelaya**: La Barra de Punta Gorda, 0–2 m, 11°30′N, 83°46′W, *Moreno 13225* (MO); Caño Montecristo, mouth of Caño El Consuelo, ca. 10 m, 11°35′N, 83°51′W, *Moreno 15027* (MO); 6.5 km al SE de Waslala, 520–560 m, 13°16′N, 85°24′W, *Moreno 17288* (MO); Puerto Cabezas–Rosita, ca. km 47, ca. 5.3 km W of Río Wawa Ferry, <10 m, 14°06′N, 83°35′W, *Stevens 8568* (MO); along road to Panua, 2.3–3.1 km NW of Panua, 4.2–5 km from main road, 30–40 m, 14°18–19′N, 83°41–42′W, *Stevens 7796* (MO); Puerto Cabezas–Río Wawa, Ibo Tingni, drainage of Caño Sung Sung, <10 m, 14°9–11′N, 83°29–31′W, *Stevens 10658-a* (MO); Auastara vicinity, <10 m, ca. 14°19′N, 83°12–13′W, *Stevens 10441* (MO); SW of Bluefields, 10–40 m, 12°N, 83°46′W, *Stevens 19781* (MO); 6.3 km S of bridge at Colonia Yolania, on road to Colonia Manantiales of Nueva Guinea, 200–300 m, *Vincelli 249* (MO); 40–45 km SW of Waspam, 10–100 m, *Atwood 3717* (MO); Cerro Livico, 7 km NE of Siuna, 500 m, *Neill 3634* (BM, MO); Cerro Waylawás, ca. 80 m, 13°39′N, 84°49′W, *Pipoly 4370* (MO); ca. 100–200 m, 13°38–39′N, 84°48–49′W, *4239* (MO); *4162* (MO); ca. 100–268 m, ca. 13°39′N, 84°48–49′W, *Stevens 7378* (MO); Caño Costa Riquita, ca. 1.8 km SW of Colonia Naciones Unidas, 150–180 m, ca. 11°43′N, 84°18′W, *Stevens 5081* (MO); Cerro Saslaya–San José del Hormiguero, between Caño Sucio and Loma Mollejones, ca. 300–450 m, 13°45′N, 84°58–59′W, *Stevens 7011* (MO); Cayo Palmeta, 0–10 m, 11°34′N, 83°39′W, *Stevens 20765* (MO); San Juan del Norte, *Smith 22* (MO); *Seymour 5906* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–320 m, 13°40′N, 84°30′W, *Pipoly 4846* (MO); Estación Experimental El Recreo, W de Cerro La Ceiba, 12°10′N, 84°18′W, *Sandino 1656* (MO); Monkey Point, Caño El Pato, ca. 10 m, 11°35′N, 83°42′W, *Moreno 12399* (MEXU, MO); 1–5 m, 11°36′N, 83°40′W, *12318* (MO); 1–5 m, 11°36′N, 83°38′W, *Moreno & Sandino 12007* (MO); 0–20 m, 11°35′N, 83°39′W, *Stevens 20031* (MO); 1 km S of Monkey Point, ca. 5 m, 83°39′W, 11°35′N, *Moreno & Sandino 12541* (MO); Río Likas, near Silima Lila, 50 m, ca. 14°30′N, 83°50′W, *Pipoly 4097* (MO); Río Prinzapolka, 0.3–1.9 km N of Limbaika, 8–10 m, ca. 13°29′N, 84°13′W, *Stevens 8264* (MO); ca. 2 km S of Waní, ca. 0–100 m, ca. 13°42′N, 84°50′W, *Pipoly 4729* (MO); Río Punta Gorda, Atlanta, 10 m, 11°33′N, 84°02′W, *Moreno & Sandino 12808* (MO); Atlanta, 2 km S of Carolina del Sur, ca. 60 m, 11°32′N, 84°01′W, *Moreno & Sandino 12890A* (MO); Río Rama, Caño Zamora, ca. 10 m, 11°57′N, 84°16′W, *Stevens 8849* (MO); Río Sucio, E of Bonanza, ca. 140 m, 14°01′N, 84°34′W, *Stevens 12345* (MO); Río Waspuk, 75–100 m, 14°15′N, 84°36′W, *Stevens*

13091 (MO). PANAMA. Ahorca Lagarto, *Cowell 262* (NY). **Bocas del Toro**: Gualaca–Chiriquí Grande, 4.2 mi. S of Chiriquí Grande, 8°55′N, 82°09′W, *Croat 66816* (AAU, CM, F, MO); Changuinola–Almirante Railroad, Milla 7.5, 100 m, *Croat & Porter 16433* (MO); *Croat 38122* (MO); Chiriquí Lagoon, Water Valley, *von Wedel 989* (GH, MO); Isla Colón, Swan Key, 2 km N, *Tyson & Loftin 6307* (FSU, MO); Río Cricamola, Finca St. Louis–Konkintoë, *Woodson et al. 1901* (GH, MO, NY); Río Changuinola, ca. 1 km above mouth of Río Teribe, <100 m, 9°21′40″N, 82°31′40″W, *Croat & Zhu 76446* (CM, MO). **Canal Area**: *Hayes 805* (NY); Gorgona–Gatún, 10–15 m, *Pittier 2300* (US); Gatún, *Standley 27023* (US); Ft. Sherman, *Standley 30992* (US); Frijoles, *Standley 27467* (US); Ft. Randolph, *Standley 28626* (US); 66–70 m, *Dodge et al. 16870* (MO, U, UC); near Gatún, *Standley 27203* (US); vic. Summit Garden, *Tyson & Lazor 6121* (FSU, RSA); Barro Colorado Island, Gatún Lake, *Standley 31328* (US); *40818* (US); *Kenoyer 178a* (US); *Elmore X14* (MICH, RSA, US); *Croat 7178* (MO); 79°49′46″W, 9°09′56″N, *6124* (MO, NY, SCZ); *6060* (MO); *4655* (MO, SCZ); *Aviles 44* (MO); *Shattuck 266* (GH, MO); Navy Pipeline Road, *Smith & Smith 3313* (US); 0.25 km NW of Río Macho bridge, 10 km NW of Gamboa, 125 m, *Nee 7863* (MO, RSA, TEX). **Chiriquí**: Gualaca–Chiriquí Grande, 13.6 mi. N of Continental Divide, 120 m, 8°57′N, 80°56′W, *Croat 74934* (MO). **Coclé**: 27 km N of Penonomé, on road to Coclesito, at Continental Divide, 1500 ft., *Hammel 1648* (SEL, MO); Llano Grande–Coclesito, 12 mi. from Llano Grande, 200 m, 8°47′N, 80°28′W, *Churchill et al. 3987* (RSA). **Colón**: ca. 8 km E of Piña, 50–100 m, 9°17′N, 80°W, *Thompson 4815* (CM, MO); Río Indio–Miguel de la Borda, 0 m, *Croat 36927* (MO); near Nuevo Tonosí, 2 mi. from Portobelo, on road to Nombre de Dios, <100 m, *Croat 33527* (MO); Santa Rita Ridge, Transisthmian Highway, ca. 10 mi. from hwy., *Porter et al. 4738* (MO); ca. 7 mi. from Transisthmian Highway, ca. 650 ft., *Wilbur et al. 15083* (MO); Santa Rita Trail, *Cowell 106* (NY). **Panamá**: ca. 20 km from Inter-American Highway, N of Cerro Azul, *Mori et al. 3786* (MO); Río Terabe Valley, El Llano–Cartí, 8 km from Pan-American Highway, 300–400 m, 9°16′N, 79°W, *Knapp & Schmalzel 5476* (MO). **San Blas**: Isla Playón Chico, 0–50 m, 9°20′N, 78°13′W, *Herrera 369* (MO); Nusagandi, El Llano–Cartí Road, 9 mi. N of main highway, 350 m, 9°20′N, 79°W, *Croat & Zhu 76566* (MO, SEL). **Veraguas**: Santa Fe–Río Calovébora, 0.6 mi. beyond agricultural school near Santa Fe, 735 m, *Croat 32982* (MO).

Philodendron radiatum var. **pseudoradiatum** (Matuda) Croat, stat. et comb. nov. Basionym: *Philodendron pseudoradiatum* Matuda, Revista Soc. Mex. Hist. Nat. 1: 96, fig. 8. 1950. TYPE: Mexico. Chiapas: Mun. Escuintla: Turquía, Salto de Agua, 8 Sep. 1947, *Matuda 17787* (holotype, MEXU; isotypes, DS, NY, UC). Figures 8, 327–330.

Internodes 2–12 cm long, 1–2.5 cm diam.; cataphylls unribbed; **petioles** 28–78 cm long; **blades** shallowly lobed, the divisions near the middle of the blade extending less than ½ the way to midrib, 11–60 cm long, 11–42 cm wide; posterior lobes (8)12.5–25 cm long, (9)16.2–18 cm wide; basal veins 5(7–8) per side, with 0–1 free to base, posterior rib absent; primary lateral veins 3–5 per side. INFLORESCENCES 1 per axil; **spathe** 12–18 cm long; **spadix** 12.8–17 cm long; pistillate portion 4–4.5 cm long; pistils 1.6–2.2 mm long; ovary with sub-basal placentation; style similar to style type B.

The flowering phenology of *Philodendron radiatum* var. *pseudoradiatum* is still poorly known. Flowering collections are known only from January and September, but the flowering pattern is probably just poorly documented rather than bimodal.

Philodendron radiatum var. *pseudoradiatum* is endemic to Mexico, where it is known only from southwestern Chiapas, at 200 to 350 m elevation in "Selva Alta Perennifolia."

Philodendron radiatum var. *pseudoradiatum* is distinguished by its incised-lobate blades with the lobes divided less than halfway to the midrib. The typical variety generally has the blades incised more than three-fourths of the way to the midrib.

This taxon might be confused with *P. dressleri*, which also has leaf blades divided only about halfway to the midrib. That species differs in having much thicker stems (typically to 6 cm diam.), sharply 2-ribbed cataphylls, and by occurring in much drier areas where it loses its leaves during the dry periods. In contrast, *P. radiatum* var. *pseudoradiatum* has rather slender stems, unribbed cataphylls and occurs in mesic areas.

Until recently, *Philodendron radiatum* var. *pseudoradiatum* was represented by only two collections, *Matuda 17787* and *18718*, from the same locality. Several collections are noteworthy. *Matuda 18045* consists of two sheets, one of which has a leaf lobed in much the same manner as the type, while the other has a leaf lobed to more than two-thirds of the way to the midrib. This may be an indication that the type of *P. radiatum* var. *pseudoradiatum* is merely an aberration in the degree of lobing for *P. radiatum*.

Another noteworthy collection is *Croat & Hannon 63381* from Sierra de Soconusco, northwest of Mapastepec. It is perhaps also *P. pseudoradiatum* but has smaller and narrower leaves. It looks much like a hybrid between *P. radiatum* var. *pseudoradiatum* and some other species, but if so, it is not clear which other species might be involved in the putative hybrid plant.

Additional specimens examined. MEXICO. **Chiapas**: Escuintla, Salto de Agua, 350 m, *Matuda 18718* (MEXU, UC); Mpio. Mapastepec, Sierra de Soconusco, new unfinished road to Tuxtla Gutiérrez, 200 m, 15°31′N, 92°50′W, *Croat & Hannon 63381* (CAS, CM, F, MEXU, MO, TEX).

Philodendron roseospathum Croat, sp. nov. TYPE: Panama. Panamá: Cerro Jefe, along road just below the summit, 9°15′N, 79°30′W, 17 June 1976, *Croat & Zhu 76211* (holotype, MO–4619415; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, GH, HUA, K, M, MEXU, NY, P, PMA, RSA, S, SEL, TEX, US, VEN). Figures 341–345.

Planta terrestris, raro hemiepiphytica; internodia 1–4 cm longa, 1.5–2.7 cm diam.; cataphylla 12–27 cm longa, acute 2-costata, persistentia semi-intacta nodis superioribus; petiolus U-formatus, obtuse sulcatus, 10–23 cm longus, 3–6 mm diam., crassior quam latus; lamina (22)30–49 cm longa, 9.8–21 cm lata, elliptica vel oblongo-elliptica, interdum oblanceolata, interdum attenuata apice, acute vel anguste rotundata, interdum attenuata basi; inflorescentia 1–2; pedunculus 2.5–6 cm longus; spatha 6.5–10 cm longa; lamina spathae extus saepe rubella plerumque atriviridi, intus pallide viridi vel marronina; tubo spathae extus pallido-lineato, intus pallide viridi vel marronino; pistilla (4)5–7(8)-locularia; loculi 14–18-ovulati; baccae albae.

Terrestrial or rarely hemiepiphytic; stem appressed-climbing or creeping, leaf scars inconspicuous, obscured by cataphyll fibers; internodes short, semiglossy, 1–4 cm long, 1.5–2.7 cm diam., longer than broad, dark green to gray-green to reddish, obscured by cataphyll fibers; roots many, thin, wiry, descending, greenish brown; cataphylls 12–27 cm long, sharply 2-ribbed (unribbed to weakly to sharply 2-ribbed in Colombia), pale red to purple-violet, drying dark brown, sharply D-shaped, persisting semi-intact at upper nodes, as fibers below; **petioles** 10–27 cm long, 3–6 mm diam., U-shaped, thicker than broad, firm, dark green to reddish, tinged purple, somewhat flattened to obtusely or narrowly sulcate adaxially; geniculum pale green to reddish violet, 1 cm long, 1.5 cm diam.; **blades** elliptic to oblong-elliptic, sometimes oblanceolate, rarely elliptic, coriaceous to subcoriaceous, conspicuously bicolorous, sometimes acuminate at apex (the acumen inrolled, 1–3 mm long), acute to narrowly rounded, sometimes attenuate at base, (22)30–49 cm long, 9.5–21 cm wide (1.8–3.5(4.5) times longer than broad), (1.6–3.2 times longer than petiole), about twice as long as wide, upper surface dark green, matte to semiglossy, lower surface moderately paler, semiglossy to glossy; midrib narrowly sunken, paler than surface above, narrowly convex, thicker than broad, matte, paler than surface and sometimes reddish green below; basal veins lacking or sometimes 1–2 per side, free to base; primary lateral veins 8–14(16) per side, departing midrib at a 40–55° angle, sunken to narrowly sunken, concolorous to paler than surface above, convex and darker than surface below; interprimary veins few, sunken to narrowly sunken, concolorous to paler than surface above, raised and darker than surface below; minor veins few, moderately obscure above, darker than surface below, arising from midrib only, sometimes prominulous and weakly undulate on drying. INFLORESCENCES 1–2 per axil; peduncle 2.5–6 cm long, 2.5–5 mm diam., reddish, prominently green streaked; **spathe** 6.5–10 cm long (1.3–3.3(4.6) times longer than peduncle), red to maroon or violet-purple or sometimes green heavily tinged red, sometimes greenish white throughout; spathe blade frequently dark green (red in Colombia) outside, pale green to maroon inside; spathe tube short pale-lineate outside, 3–4 cm long, 2 cm diam., pale green to maroon inside; **spadix** ± tapered, 6.8–8 cm long, broadest at the base; pistillate portion white to pale green, cylindrical, 2–3.7 mm long, 1–1.5 mm diam. at apex, 11–7.2 mm diam. at middle, 9–11(17) mm wide at base; staminate portion 3.9–4.9(6) cm long; fertile staminate portion cream, cylindrical to somewhat tapered, 10 mm diam. at base, 8 mm diam. at middle, 8 mm diam. ca. 1 cm from apex, broadest usually at base, narrower than the pistillate or sterile portion; sterile staminate portion as broad as the pistillate portion, 10 mm diam.; pistils 2.5 mm long, 1.6–1.9 mm diam., tinged reddish; ovary (4)5–7(8)-locular, 1.4 mm long, 1.6 mm diam., with axile placentation; locules 1.4 mm long, 0.5 mm diam.; ovules 14–18 per locule, contained within a gelatinous matrix, 2-seriate, 0.3–0.5 mm long, longer than funicle; funicle 0.2–0.4 mm long, adnate to lower part of partition, style 0.4–0.6 mm long, 1.6–1.8 mm diam., similar to style type B; style apex flat to weakly rounded; stigma usually subdiscoid, 1.1–1.3 mm diam., 0.2–0.5 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.7 mm long, 1.2–1.5 mm diam. at apex; thecae oblong to cylindrical, 0.5 mm wide, ± parallel to one another and contiguous; sterile staminate flowers clavate, blunt, irregularly 4–6-sided, 2.3 mm long, 2 mm wide. INFRUCTESCENCE with pistillate spadix 4–4.5 cm long, 1.5–2.5 cm diam.; berries white (immature), 3.5 mm long, 2.6 mm diam., 12–14 per locule; seeds 7–9 per locule, whitish, oblong, 1.8 mm long, sharply tapered on one end.

Philodendron roseospathum ranges from Panama to Colombia. In Panama, this taxon is restricted to both sides of the Panama Canal, ranging from Ver-

aguas to San Blas, mostly in *Premontane rain forest* or less frequently in *Tropical wet forest* life zones, at 350 to 1000 m elevation. In Colombia, it has been collected only in tropical pluvial forest at 100 to 900 m.

Philodendron roseospathum is a member of *P.* sect. *Philodendron* subsect. *Canniphyllum*. The typical variety is recognized by its generally erect, frequently terrestrial habit, short internodes, and rosulate cluster of leaves with moderately short, bluntly sulcate, thicker-than-broad petioles. The dark green, elliptic-oblanceolate leaf blades are narrowly rounded to acute at the base. It is especially recognizable by its masses of weathered persistent cataphylls and clusters of inflorescences with reddish spathes (hence the name "roseospathum"). This species is unusual for the genus in that it is generally terrestrial. It has prospered in cultivation and is deemed an important horticultural introduction.

Philodendron roseospathum appears to be most closely related to *P. cuneatum* Engl. from the Pacific slope of Colombia, but the latter species differs in having acutely sulcate, C-shaped petioles and smaller, more narrowly pedunculate inflorescences with white spathe blades. It is also related to several other undescribed species from the Amazon basin.

Philodendron roseospathum is here divided into two varieties, with variety *angustilaminatum* Croat differing from the typical variety in having somewhat longer petioles and proportionately much narrower blades (4.5 times longer than broad vs. an average of 2.5 times longer than broad for the typical variety). See *P. roseospathum* var. *angustilaminatum* for additional differences.

KEY TO THE VARIETIES OF *P. ROSEOSPATHUM*

1a. Blades oblong, ca. 4.5 times longer than wide; Panama (Colón), 915 m elevation ..... var. *angustilaminatum*

1b. Blades ± elliptic, ca. 2.5 times longer than wide; Panama to Colombia, 400–900 m elevation ..... var. *roseospathum*

Philodendron roseospathum Croat var. **roseospathum**

Flowering in *Philodendron roseospathum* var. *roseospathum* occurs in the late dry season and early rainy season (March through July) with post-anthesis collections known from March through September and immature fruits from July to December. The few South American collections concur with this pattern. Flowering collections are known from Colombia in July.

In Central America, *P. roseospathum* var. *roseospathum* is common locally in cloud forests along the Continental Divide as far west as Veraguas and as far east as the El Llano-Cartí Road. It is certainly to be expected in Darién Province.

For differences with *P.* var. *angustilaminatum*, see the preceeding key.

Additional specimens examined for P. roseospathum *var.* roseospathum. PANAMA. **Coclé**: Continental Divide ridge, Coclesito Road, *Hammel 2540* (CR, MO); El Copé region, 7 km N of Copé, Alto Calvario, 800 m, *Folsom & Mauseth 7948* (MO); 750–900 m, *Croat 44738* (F, MO); 710–800 m, 8°39′N, 80°36′W, *68763* (MO); 900–1000 m, 8°39′N, 80°36′W, *Croat 75057* (MO); El Valle region, La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *Croat 67130* (CAS, CM, K, MEXU, MO, NY, PMA, TEX); 860–900 m, *37346* (F, MO); 830–900 m, 8°36′N, 80°07′W, *74810* (CM, LE, MO, WIS); ca. 800 m, *25435* (F, MO); *Luteyn & Kennedy 1652* (MO); 850 m, 8°37′N, 80°06′W, *de Nevers et al. 3513* (MO); 2700 ft., *Sytsma et al. 4350* (CM, MO); 840–880 m, 8°38′N, 80°7.5′W, *Grayum & Evans 9908* (MO); Cerro Gaital, 900–1000 m, 8°40′N, 80°07′W, *Knapp 5311* (MO); 860 m, 8°37′N, 80°08′W, *Croat & Zhu 76734* (AAU, CAS, CM, MEXU, MO); N slope and summit of Cerro Pilón, 900–1173 m, *Croat 22951* (MO). **Panamá**: El Llano–Cartí Road, 4 mi. beyond the highway, 500 m, *Croat 49135* (MO); Cerro Jefe region, 750–850 m, 9°15′N, 79°30′W, *McPherson 11166* (MO), *11197* (CM, MO); 1000 m, *Croat 49088* (MO); ca. 1000 m, *Mori et al. 3795* (MO); ca. 950 m, ca. 9°15′N, 79°30′W, *McPherson 7107* (B, K, MO, US); 2500–3000 ft., *Hammel 3704* (MO); 750–800 m, 9°14′N, 79°22′W, *Croat 67089* (MO); vic. Altos de Pacora, 800–1000 m, *Croat 22672* (CM, L, MO, WIS); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68635* (MO); La Eneida, ca. 800 m, *Kennedy et al. 3374* (US); *Plowman & Weil 3158* (ECON); 1000 m, *Folsom & Page 5938* (MO); 6 mi. above Lago Cerro Azul, *Croat 15225* (MO); Campo Tres, ca. 700 m, *Croat 27069* (F, MO); 4.6 km beyond peak, on road to Altos de Pacora, 26.3 km from the Inter-American Highway, ca. 600 m, *Croat 35931* (CAS, CM, F, GH, M, MEXU, MO, P). **San Blas**: El Llano–Cartí Road, Nusagandi, 300–350 m, 9°15′N, 79°W, *Croat 69282* (MO); Mile 10.9, 450 m, 9°18′N, 79°59′W, *Croat 75123A* (MO); Cerro Obu, 400–500 m, 400–500 m, *de Nevers et al. 8054* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río San Luis, past Escuela Agrícola Alto de Piedra, ca. 5 mi. N of school, 670 m, 8°33′N, 81°08′W, *Croat 66972* (GB, MO, RSA); Santa Fe–Calovébora, 1.7 mi. past Alto Piedra School, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76857B* (MO).

COLOMBIA. **Antioquia**: Parque Nacional Natural "Las Orquídeas," Sector Venados, 900 m, 6°33′N, 76°19′W, *Cogollo et al. 3344* (MO). **Chocó**: Quibdó–Istmina, vicinity of Quibdó, <100 m, 6°28′N, 76°36′W, *Croat & Cogollo 52233* (MO); Quibdó–Bolívar, 117–118 km E of Quibdó, 465 m, 5°44′N, 76°28′W, *Croat 57515* (CHOCO, CM, COL, JAUM, MO, NY, PMA); Río Baudó, *Fuchs et al. 22048* (COL); Medellín–Quibdó at Km 208.5, 9 km W of Tutunendo, ca. 9 km E of Quibdó, <100 m, 5°39′N, 76°40′W, *Croat 56202*.

Philodendron roseospathum Croat var. **angustilaminatum** Croat, var. nov. TYPE: Panama. Colón: Cerro Bruja as approached from Río Escandaloso, 915 m, 18 May 1978, *Hammel 3133* (holotype, MO–2639732). Figure 349.

Internodia brevia; cataphylla ignota; petiolus 24–27 cm longus; lamina oblonga, 42–46 cm longa, 9.5–10 cm lata, circa duplo longior quam petiolus; pedunculus 3.8 cm longus; spatha 7 cm longa, omnino viridalba; pistilla (4)5-locularia; loculi 6–8-ovulati.

Internodes short; cataphylls not seen; **petioles** 24–27 cm long; **blades** oblong, acuminate at apex, rounded at base, 42–46 cm long, 9.5–10 cm wide (4.2–4.8 times longer than wide), (1.75 times longer than petiole); basal veins 2 per side, free to base; primary lateral veins 10 per side. INFLORESCENCES with peduncle 3.8 cm long; **spathe** 7 cm long greenish white throughout; spathe tube 3 cm long; **spadix** 6.3 cm long; pistillate portion 2 cm long in front; staminate portion 4.3 cm long; pistils 1.7 mm long; ovary 4(5)-locular; ovules 6–8 per locule, 1-seriate, ca. 0.3 mm long; style similar to style type D. Berries unknown.

Flowering in *Philodendron roseospathum* var. *angustilaminatum* probably occurs in the wet season, with the only flowering collection from May.

Philodendron roseospathum var. *angustilaminatum* is known only from the type locality near the Canal Area in Colón Province, at 915 m elevation in *Premontane rain forest.*

This variety is distinguished by its long-petiolate, oblong leaf blades with rounded bases and greenish white spathes. It is distinguished from the typical variety by its proportionately much narrower blades (4.5 times longer than wide in *P. roseospathum* var. *angustilaminatum* vs. about 2.5 times longer than wide in var. *roseospathum*) and proportionately longer petioles (only 1.7 times longer than petiole vs. 1.6–3.2 times longer in var. *roseospathum*). In addition, *P. roseospathum* var. *angustilaminatum* has only 6–8 ovules per locule (vs. 16–18 for *P. roseospathum* var. *roseospathum*).

It is unusual that *P. roseospathum* var. *angustilaminatum* has style type D while the autonymic variety has style type B. Perhaps it is an artifact of the poorly preserved nature of the material.

One collection, *Croat 57592,* from near Queremal in Valle Department, at 1300 m in an area of either *Premontane moist forest* or *Tropical Lower Montane wet forest,* may also represent this variety but has unribbed cataphylls. *Croat 57036,* a sterile collection from Cotopaxi Province, Ecuador, also has unribbed cataphylls and may represent the same taxon.

Philodendron rothschuhianum (Engl.) Croat & Grayum, Ann. Missouri Bot. Gard. 74: 659. 1987. *Syngonium rothschuhianum* Engl., in Engl. & K. Krause, Pflanzenr. IV. 23E (Heft 71): 124. 1920. TYPE: Nicaragua. Matagalpa: Matagalpa, 1000 m, 12°55′N, 85°55′W, *Rothschuh 229* (holotype, B). Figures 4, 9, 31, 336–340, 347, 348.

Hemiepiphytic to epiphytic or rarely terrestrial; stem appressed-climbing, creeping, sap watery, leaf scars conspicuous, 2 cm long, 2.5 cm wide; internodes short, semiglossy, 1.8–3 cm long, 1.5–3 cm diam., about as long as broad, gray-green, epidermis fissured; roots scurfy, few per node; cataphylls fleshy, soft, 16–23 cm long, unribbed then sharply 2-ribbed at apex, or bluntly 2-ribbed throughout or weakly 1-ribbed throughout, green, short dark striate, semiglossy, deciduous, emarginate with subapical apiculum at union of ribs at apex. LEAVES erect-spreading to spreading; **petioles** 33–71 cm long, 3–13(20) mm diam., subterete, moderately spongy, medium green, obtusely 1-ribbed near apex adaxially, surface weakly glossy, densely green striate; sheath inconspicuous; **blades** deeply 3-lobed, subcoriaceous, weakly bicolorous, gradually acuminate, long to very long acuminate at apex (the acumen inrolled, 1–2.5 mm long), ± hastate at base, 22–42 cm long, 25–57 cm wide (0.6–1 times longer than wide), (0.5–1 times the petiole length), about two-thirds as long as petiole, upper surface semiglossy, lower surface weakly glossy, slightly paler; sinus hippocrepiform; median lobes 16–39.5 cm long, 7–20 cm wide; lateral lobes narrowly ovate, 14–28 cm long, 5–17 cm wide, directed toward apex, broadly confluent 2–5 cm with medial lobe, the margins undulate; midrib sunken to narrowly concave, paler than surface above, almost round-raised, paler than surface below; basal veins 10–15 per side, the remainder arranged in a ± regular manner in the posterior lobe, coalesced in part throughout much of their length into a central rib; posterior rib usually not naked, sometimes naked for 1 cm, rarely to 2.5 cm; primary lateral veins 5–12 per side, departing midrib at a 50–65° angle, narrowly sunken, concolorous above, convex below; interprimary veins sunken and concolorous above, raised, almost as conspicuous as primary lateral veins below; minor veins darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2–3(9) per axil; peduncle 5.2–21 cm long, 5–10 mm diam., medium green, densely lineate; **spathe** (6.5)8–14(16) cm long, (0.6–2.2 times longer than peduncle), markedly constricted above the tube; spathe

blade pale green to greenish white to yellowish green outside, to ca. 5 cm wide when open, ca. 2.4 cm diam. at constriction, greenish white to creamy white inside; spathe tube ellipsoid, 4–7 cm long, pale green to yellowish green outside, greenish to greenish white to creamy white inside; **spadix** very short stipitate; somewhat protruding forward at anthesis, 10.5 cm long, constricted at base of fertile staminate portion; pistillate portion pale lime-green, 3.7 cm long in front, 2.5 cm long in back, 1–1.3 cm diam. at apex, 1.2–1.4 cm diam. at middle, 1.2 cm wide at base; staminate portion 6.4–9.3 cm long; fertile staminate portion creamy white, clavate, 1 cm diam. at base, 1.3 cm diam. at middle, 1 cm diam. ca. 1 cm from apex, usually broader than the pistillate portion; sterile staminate portion broader than fertile or pistillate portion, creamy white, 1.6–1.9 cm diam. at base, 1.3–1.4 cm. diam. at apex; pistils 1.6–2.6 cm long, 1.2 mm diam.; ovary 5–7-locular, 0.8 mm long, 1.1 mm diam., with sub-basal placentation; locules 0.8 mm long, 0.3–0.4 mm diam.; ovule sac 0.6 mm long; ovules 1 per locule, contained within translucent, gelatinous ovule sac, 0.3–0.5 mm long, longer than funicle; funicle 0.1–0.3 mm long (can be pulled free to base), style 0.6 mm long, 1.2 mm diam., similar to style type B; style apex sloping to rounded; stigma brush-like, hemispheroid, 0.7–1 mm diam., 0.3–0.6 mm high, covering entire style apex; apex drying button-like, with or without radial ridges from center; the androecium truncate, oblong, ± prismatic, margins irregularly 4–6-sided, 1–1.6 mm long, 1.5–1.9 mm diam. at apex; thecae oblong, 0.4 mm wide, ± parallel to one another, nearly contiguous; sterile staminate flowers blunt, sometimes clavate or prismatic or irregularly 5–6-sided or 3–6-sided, 1.7–2.3 mm long, 1.6 mm wide. Berries pale green or pale yellow-green to greenish white, 4 mm long, 2.5 mm diam.; seeds 1–3, medium green, (1.2)2.1–2.3 mm long, 0.6–0.8 mm diam., within thin envelope. JUVENILE plants with petioles sheathed to about midway; blades with posterior lobes hastate, acuminate at apex, promptly auriculate on posterior margin, broadly confluent with anterior margin on anterior margin.

Flowering in *Philodendron rothschuhianum* occurs during the dry season and early rainy season. Most collections have been made in March, but flowering occurs as late as August. Post-anthesis collections have been made from January through November (except October), but are particularly abundant from March through May. Immature fruiting collections have been made from April through September (also December), but mature fruits are known from only August.

Philodendron rothschuhianum ranges from Honduras (Gracias a Dios) and from Nicaragua (Río San Juan, Zelaya, Jinotega, and Matagalpa) to Panama (Bocas del Toro, Veraguas, and Coclé), principally on the Atlantic slope, from sea level to 1450 (mostly less than 1000) m elevation. It occurs in *Premontane wet forest, Tropical wet forest,* and less frequently in wetter parts of *Tropical wet forest* and *Premontane rain forest* life zones.

Philodendron rothschuhianum is a member of *P.* sect. *Tritomophyllum.* This species is distinguished by its short internodes; unribbed, deciduous cataphylls; subterete, moderately spongy petioles; and especially by its deeply three-lobed blades about two-thirds as long as the petioles with the lateral lobes broadly confluent with the medial lobe and the sinus hippocrepiform and naked along the posterior rib for a short distance from the petiole.

Philodendron rothschuhianum is most frequently confused with *P. tripartitum,* which differs in having less auriculate lateral lobes that are scarcely or not at all naked along the posterior rib. In addition, *P. tripartitum* has a much more slender, scarcely constricted, spathe tube reddish within (vs. a markedly inflated, uniformly greenish tube in *P. rothschuhianum*).

In terms of leaf shape, *P. rothschuhianum* is closest to *P. cotobrusense.* The latter differs in medial lobes with 18–19 pairs of primary lateral veins (vs. 5–12 pairs for *P. rothschuhianum*).

The style apex is apparently variable in this species, with *Croat 66772* and *Neill 1569* having type B styles while *Croat 35657* has style type D. The latter has the style apex prolonged into a distinct boss separated from the rest of the style apex by a distinct neck.

Additional specimens examined. COSTA RICA. **Alajuela**: Quebrada Guillermina, on N side of Volcán Arenal, 500 m, 10°29′N, 84°42′W, *Lent et al. 3415* (F, U); Naranjo–Aguas Zarcas, 8 km NE of Quesada, 600 m, *Croat 46942* (MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, *Croat 43567* (MO); *43637* (MO); Monteverde Biological Reserve, Río Peñas Blancas, 800 m, *Bello 1980* (CR, INB); 850–900 m, 10°20′N, 84°43′W, *Haber & Bello 6836* (MO); 850 m, 10°19′N, 84°43′W, *Haber & Cruz 8409* (MO); Finca de Tomás Guindon, 900 m, 10°19′N, 84°43′W, *Bello 763* (CR, MO); Río Sarapiquí, road to Colonia Virgen del Socorro, ca. 740 m, 10°5.5′N, 84°10.5′W, *Grayum & Hammel 5516* (B, CR, MO); ca. 800 m, *Burger & Antonio 11101* (CR, F); *11097* (F); 830 m, *Croat 68301* (MO); Vara Blanca–Puerto Viejo, 3 mi. N of San Miguel, 380 m, *Croat 35657* (CR, MO); Cañas–Upala, 3 km NNE of Bijagua, 450 m, 10°45′N, 85°3′W, *Burger & Baker 9881* (CR, F); 8 km N of Bijagua, 300 m, *Croat 36502* (CR, MO); 13.8 km N of Bijagua, 100–150 m, *Croat 36438* (MO); *36402* (CR, MO); near Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, *Croat 36402* (MO); 13 km W of Fortuna, Río Tabacón, 500–550 m, 10°29′N, 84°43′W, *Liesner et al. 15250* (MO); 15 km

NW of Arenal by air, 700 m, 10°34.5′N, 84°54′W, *Liesner et al. 15088* (MO); *15065* (MO); San Ramón, *Bittner & Venschott 1941* (CR); *Nilsson 460* (CR). **Cartago**: 4 km SE of Pejibaye, 700 m, 9°48′N, 83°42′W, *Liesner et al. 14330* (MO); Turrialba, *León 393* (US). **Guanacaste**: Parque Nacional Guanacaste Estación Pitilla, 600 m, 11°02′N, 85°25′18″W, *Hammel et al. 17372* (CR, MEXU, MO, NY, U, USJ). **Heredia**: near Tirimbina, E of Río Sarapiquí, 150–250 m, 10°24′N, 84°7′W, *Burger & Burger 8026* (F); Tirimbina, 700 ft., *Proctor 32148* (LL); La Selva Field Station, 100 m, *Jacobs 2826* (DUKE); *Folsom 9874* (DUKE); 50–80 m, 10°26′N, 84°01′W, *Grayum & Chavarria 8300* (MO); Puerto Viejo de Sarapiquí, *Grayum 2120* (DUKE); ca. 100 m, *Grayum 2856* (MO); *Croat 57199* (MO, voucher of live plant of *Grayum 2856*); Río Puerto Viejo, ca. 2 km upstream from confluence with Río Sarapiquí, 100 m, 10°26′N, 84°10′W, *Burger & Stolze 5756* (CR, US); Volcán Barva, Río Peje–Río Sardinalito, 700–950 m, 10°17.5′N, 84°04.5′W, *Grayum 6981* (CR, MO); 700–800 m, 10°17.5′N, 84°04.5′W, *6720* (CR, MO). **Limón**: ca. 1 mi. NE of Bribrí, ca. 40 mi. SW of Limón, above Río Catarata, 50–100 m, *Croat 43245* (MO); 7 km SW of Bribrí, 100–250 m, *Gómez et al. 20320* (MO); Río Pacuare, 50–100 m, 10°05′N, 83°29′W, *Burger & Liesner 6895* (F, MO); vic. of Guápiles, 300–500 m, *Standley 37469* (US); 2 km W of Río Toro Amarillo, W of Guápiles, 275 m, 10°13′N, 83°50′W, *Thompson & Rawlins 1216* (CM); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson et al. 7138* (RSA); Bahía de Portete Parque Nacional, 0–10 m, 10°N, 83°05′W, *Thompson & Rawlins 1176* (CM); Cerro Coronel, E of Río Zapote, along and above new road, within 1 km of Río Colorado, 10–40 m, 10°40′N, 83°40′W, *Stevens 24277* (CR, MO); E of Río Zapote, 10–100 m, 10°40′N, 84°40′W, *Stevens 23974* (CR, MO); E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 24453* (CR, MO); Parque Nacional Tortuguero, Puesto Cuatro Esquinas, 4 m, 10°32′N, 83°30′W, *Robles 1837* (CR, MO); Barra del Colorado, 0–2 m, 10°47′N, 83°35′W, *Stevens 24073* (CR, MO); Río Colorado, Barra del Colorado, 1–5 m, 10°47′40″N, 83°35′30″W, *Davidse & Herrera 30869* (MO); 2 airline km SSE of Islas Buena Vista, 10–120 m, 10°40′N, 83°40′W, *Davidse & Herrera 31035* (MO); Río Reventazón, Finca Montecristo, below Cairo, ca. 25 m, *Standley & Valerio 49027* (US); Parque La Amistad, Fila Tsiurábeta, between Río Urén and Río Lari, 800 m, 9°27′30″N, 83°W, *A. Chacón 294* (CR, MO). **Puntarenas**: hills above Santa Elena, 3 km N of Monteverde, 1450 m, 10°20′N, 84°50′W, *Haber & Bello 5067* (MO). **San José**: S of San José, *Greenman & Greenman 5353* (MO); Braulio Carrillo National Park, Fila Carrillo, 700 m, *Gómez et al. 21149* (CR, MO); 600–700 m, *Croat 78777* (CR, INB). HONDURAS. **Gracias a Díos**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9146* (CM, MO, NY, UNAH). NICARAGUA. **Chontales**: Cerro Buenavista, 5 km N of Cuapa, *Neill 637* (MO); 4 km NW of Santo Domingo, 280 m, ca. 12°17′N, 85°06′W, *Grijalva et al. 3771* (MO). **Jinotega**: Finca San Luis, 21 km from Valle del Cuá, NW de El Cedro, 700 m, 13°30′N, 85°38′W, *Moreno 959* (MO); Río Bocay, Caño Litutus, ca. 175 m, ca. 13°58′N, 85°21′W, *Stevens et al. 16617* (MO); Salto Kayaska, 190–340 m, ca. 13°51′N, 85°22′W, *Stevens et al. 16484* (F, MO). **Matagalpa**: Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradón, slopes NW of Hacienda San Sebastián, 800–1100 m, 13°14–15′N, 85°38′W, *Stevens 21258* (MO); summit of El Toma Road, *Neill 1569* (HNMN, MO); 10.5 km NW of Matagalpa, ca. 1000 m, 12°57′N, 85°51′W, *Moreno 10233* (MO); El Paraíso, 10 km de Matagalpa, 800–820 m, 12°59′N, 85°51′W, *Moreno 6607* (MO); N of Cerro Musún, near Wanawás, *Araquistain & Moreno 2741* (LE, MO); NW of Cerro Musún, near Paylo, 500–800 m, *Araquistain & Moreno 2572* (MO); 800–1200 m, *2510* (MO); *2495* (CAS, HNMN, MO); 300–600 m, *2471A* (MO); Río Bilampí, NW of Cerro Musún, 4 km SW of Wanawás, 200–500 m, 13°00–01′N, 85°14′W, *Araquistain & Moreno 2614* (HNMN, MO, US); Comerca Wanawás, 180–200 m, 12°02–03′N, 85°13′W, *Araquistain & Moreno 2398* (HNMN, K, MO); near Cerro Musún, 8 km from Población Wanawás, Palán Grandre, 500–800 m, 12°59′–13°N, 85°14′W, *Araquistain & Moreno 2355* (HNMN, MO, NY); Río Bilampí Valley, Cerro Musún, Salto Grande of Quebrada Negra, 500–800 m, *Neill 1800* (MO). **Río San Juan**: Caño Chontaleño, 20 km NE of El Castillo (Río Indio watershed), 200 m, *Neill 3367* (MO); *Neill & Vincelli 3541* (BM, MO); Río Indio Valley, 6 km upstream from the junction with Caño La Pimienta, 300–600 m, *Neill 1557* (MO); Río Sábalo, Buenos Aires, 70 m, 11°02′N, 84°28′W, *Moreno 25595* (MO). **Zelaya**: ca. 1.5 km NE of Las Esperanza de Las Quebradas, 300–350 m, ca. 13°38′N, 85°02′W, *Stevens & Moreno 19308* (MO); Limbaika–El Empalme, ca. 3.9 km SE of El Empalme, ca. 65 m, ca. 13°39′N, 84°24′W, *Stevens 12930* (MO); road to Mina Nueva América, ca. 10 km from main road, *Stevens 12687* (MO); Rosita–Puerto Cabezas, ca. 15.7 km SW of Río Kukalaya, <100 m, ca. 13°58′N, 84°12′W, *Stevens 8500* (MO); Cerro El Inocente, near Caño Majagua, ca. 800–1000 m, ca. 13°45′N, 85°W, *Stevens 6805* (MO); Siuna–Matagalpa, ca. 31.4 km beyond Río Uli, ca. 8.9 km beyond Rosa Grande La Balsama, <200 m, *Stevens 7456* (MO); Cerro Saslaya–San José del Hormiguero, from Loma Mollejones eastward, ca. 200–400 m, ca. 13°44–45′N, 84°57–58′W, *Stevens 7049* (BM, MO); Caño Majagua, ca. 750–850 m, ca. 13°45′N, 85°00–01′W, *Stevens 6936* (MO); Caño Majagua–Caño Sucio, ca. 600–800 m, ca. 13°45′N, 84°59′–85°W, *Stevens 6821* (MO, PMA); vic. of La Pimienta, ca. 13°45′N, 84°59′W, *Pipoly 6225* (MO); Cerro La Pimienta–El Hormiguero, ca. 800–1000 m, ca. 13°45′N, 84°59′W, *Pipoly 6012* (MO); Cerro La Pimienta, number 1, ca. 900–980 m, ca. 13°45′N, 84°59′W, *Pipoly 5129* (MO); ca. 13 km above Kururia, on road to San Jerónimo, <200 m, *Pipoly 3794* (MO); Risco de Oro, ca. 40 m, *Pipoly 5043* (MO); 10 km NE of Siuna, along Caño Madriguera, 250 m, *Neill 3754* (BM, MO); 4 km NE of Siuna, road to El Dos, 300 m, 13°45′N, 84°45′W, *Moreno & Robleto 20856* (MO); 1 km W of El Naranjo, 200–210 m, 13°34′N, 85°11′W, *Moreno & Robleto 20616* (MO, QCA); SE of Cerro El Hormiguero, ca. 900–1000 m, 13°44′10″N, 84°59′50″W, *Grijalva 473* (MO); Río Iyas, Quebrada El Toro, 260–280 m, *Vincelli 370* (MO); near San Juan del Norte, *C. Smith 5* (F). PANAMA. **Bocas del Toro**: Gualaca–Chiriquí Grande, ca. 10 km SW of Chiriquí Grande, ca. 300 m, 8°52′N, 82°10′W, *Thompson 4936* (CM); 4.2 mi. S of Chiriquí Grande, ca. 0 m, 8°55′N, 82°09′W, *Croat 66815* (MO); Fortuna Lake area, Continental Divide, 900 m, 8°48′04″N, 82°15′04″W, *McPherson & Aranda 10185* (MO, PMA, W); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60276* (CM, MO, RSA); 850–950 m, 8°40′04″N, 79°50′04″W, *McPherson 10546* (AAU, M, MEXU, MO, US); ca. 300 m, ca. 8°50′N, 82°15′W, *McPherson 8522* (K, MO, US); 6.6 mi. N of bridge over Fortuna Lake, 780 m, 8°45′N, 82°18′W,

Croat 66772 (MO); 1.2 mi. N of Divide, 910 m, 8°44′N, 82°17′W, *Croat 60462* (MO, PMA); 1.6 mi. N of Divide, 850 m, 8°48′N, 82°13′W, *Croat 74931* (MO); 1.6 mi. N of Divide, 770 m, 8°45′N, 82°17′W, *Croat & Zhu 76534* (MO); Río Cricamola, Finca St. Louis–Konkintoë, ca. 10–50 m, *Woodson et al. 1919* (MO). **Coclé**: El Copé region, 4.5 mi. N of El Copé, 750 m, 8°38′N, 80°35′W, *Thompson 4760* (CM, MO); 5–6 mi. N of El Copé, 600–800 m, 8°38′N, 8°35′W, *Croat & Zhu 77224* (CM, MO); 680–770 m, 8°39′N, 80°36′W, *Croat 74828* (CM, MO); Alto Calvario, *Croat 68848* (MO). **Veraguas**: 15.6 km NW of Santa Fe, 450–550 m, *Croat 27704* (MO); 350–400 m, *27385* (MO).

Philodendron sagittifolium Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1849: 17. 1849. TYPE: Mexico. Veracruz: Río Nautla at Pital, Apr. 1841, *Liebmann s.n.* (holotype, C). Figures 346, 350–356.

Philodendron daemonum Liebm., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1849: 17. 1849. TYPE: Mexico. Veracruz: vic. Colipa at Potrero de Consoquitla, *Liebmann s.n.* (holotype, C; isotype, K).

Philodendron tanyphyllum Schott, Prod. Syst. Aroid.: 272. 1856. TYPE: Mexico. *Liebmann s.n.* (W destroyed). Schott's ic. 2557 (neotype, here designated, W).

Philodendron sanguineum Regel, Ind. Sem. Hort. Petrop. 82. 1868. TYPE: Mexico. Locality unknown: *Karwinsky s.n.* (holotype, LE? no longer extant); t. 621 in Regel, Gartenflora 18. 1869 (neotype, here designated).

Philodendron lancigerum Standl. & L. O. Williams, Ceiba 1. 232. 1951. TYPE: Costa Rica. Puntarenas: vic. Palmar Norte, Río Térraba, 30 m, *Allen 5612* (holotype, US). Costa Rica. Puntarenas: along road between Chacarita and Rincón de Osa, ca. 6 km W of Interamerican Highway at Chacarita, 160 m, ca. 8°45′N, 83°18′W, *Croat & Grayum 59728* (epitype, here designated, MO–3319112; isoepitypes, B, CR, F, K, NY, PMA, US).

Philodendron tuxtlanum G. S. Bunting, Gentes Herb. 9. 353. 1965. TYPE: Mexico. Veracruz: vic. Santiago Tuxtla, *Bunting & Davies 162* (holotype, US).

Usually hemiepiphytic, rarely terrestrial or epilithic; stem appressed-climbing, parchment-white, sap turning blackish, slimy; internodes usually terete, weakly angular, sometimes obscurely flattened on one side or closely and acutely ribbed, semiglossy to matte, 1–20 cm long, 1.5–4 cm diam., dark green, becoming usually gray-green to brown, sometimes pale yellow-green, epidermis somewhat ridged ("wrinkled"), sometimes fissured transversely; roots reddish brown, 6–10 mm long, 3–5 mm diam., arising from and along the node on one side; cataphylls 18–39 cm long, usually weakly 1-ribbed, sometimes unribbed or weakly to sharply 2-ribbed or sharply 1-ribbed (ribs to 1 cm high), soft, green, sometimes reddish to pinkish, sometimes sparsely green-spotted, purple-maroon or darker striate near base, drying reddish brown, margins sometimes prominently and thinly raised, usually soon deciduous, rarely persisting as a rotting mass, rounded at apex; **petioles** 20–65(91) cm long, 3–15 mm diam., usually subterete, moderately spongy to firm, medium green, drying greenish brown, obtusely flattened, usually obtusely and narrowly sulcate, rarely obtusely and broadly sulcate adaxially, surface minutely and densely short purple- or occasionally white-striate, sometimes dark green or violet-purple blotched, sometimes smooth to irregularly ribbed and folded; sheath subtending an inflorescence, 5–8 cm long; **blades** ovate to ovate-triangular, semiglossy, moderately coriaceous, weakly to moderately bicolorous, acuminate to narrowly acuminate, sometimes short-acuminate at apex, prominently cordate to ± sagittate at base, 30–72 cm long, 15–39 cm wide (1.85–2 times longer than wide), (0.6–1.6 times longer than petiole), margins somewhat hyaline, weakly revolute, upper surface medium green, drying brownish green to greenish brown, semiglossy, lower surface pale yellow-green, sometimes reddish, drying usually reddish brown, sometimes yellowish brown, weakly glossy to matte; anterior lobe 24–61 cm long, 13–34.5 cm wide (2–5.1(5.5–6.4) times longer than posterior lobes); posterior lobes usually narrowly rounded, 6–20.5 cm long, 5–17.6 cm wide; sinus ± V-shaped to almost closed, 6–15 cm deep; midrib flat to weakly raised, paler than surface, drying broadly raised and ± concolorous above, convex to narrowly raised, sometimes maroon-spotted or with white flecks, concolorous to darker than surface, drying broadly raised and reddish below; basal veins 3–5(6) per side, with 0–1(2) free to base, third and higher order veins sometimes coalesced 2.5–4.5 cm, a few additional veins sometimes coalesced to 6.5 cm; posterior rib not at all naked or only briefly so; primary lateral veins 4–9 per side, departing midrib at a 60–70° angle, weakly curved to the margins, but usually turned prominently up just before the margin, rather prominently downturned just before the midrib, round-raised to flat to obtusely sunken and paler than surface above, convex, concolorous to darker than surface below; interprimary veins weakly sunken, concolorous above, flat, darker than surface below; minor veins weakly visible below, arising from both the midrib and primary lateral veins, drying moderately prominent, weakly undulate, alternating with dark, mostly contiguous secretory ducts. INFLORESCENCES erect, 1–3 per axil; peduncle 4–15 cm long, 1.6–1.8 cm diam., somewhat flattened to terete, green, sometimes tinged reddish, drying greenish, densely short and broad striate; **spathe** 8–22 cm long, 2–3 cm diam. (0.8–2.2 times longer than peduncle), weakly to obscurely constricted above the tube, semiglossy, usually green, sometimes

plum-red, often purple-spotted, densely short pale lineate throughout, weakly so near apex, blunt to narrowly cuspidate-acuminate to prominently acuminate, frequently tinged purplish violet at base; spathe blade green to pale yellow-green, 8–11 cm long (opening 3–4.3 cm wide, sometimes opening to near the base), greenish white, weakly tinged red-purple in throat to pale yellow-green or white inside, sometimes reddish throughout in age; resin canals appearing as continuous lines, red-purple to orange in color; spathe tube green, sometimes moderately to heavily tinged red-purple to red (B & K red-purple 3/7.5), with sparse, dark purplish spots (mostly medially) throughout outside, 4–7 cm long, 2.5–3.5 cm diam., red to reddish purple (B & K red-purple 3/7.5), white striate inside; **spadix** stipitate to 7 mm long; tapered toward apex, (8)9–16 cm long, broadest below the middle or near the base, usually protruding somewhat forward at anthesis but not curved; pistillate portion pale green (anthesis) to greenish white to yellow-green (post-anthesis), uniformly wide throughout or weakly tapered toward both ends, 2.5–6.2 cm long in front, 2–4.7 cm long in back, 1–1.2 cm diam. at apex, 1.1–1.7(2.1) cm diam. at middle, 1.1–1.7 cm wide at base; staminate portion 6.3–10.3(13) cm long; fertile staminate portion usually creamy white, sometimes pale green to pinkish, 9–13 mm diam. at base, 11–13 mm diam. at middle, 8–10 mm diam. ca. 1 cm from apex, broadest at base or middle, about as broad as the pistillate and sterile portions; sterile staminate portion often broader than the pistillate portion, white, (0.9–1)1.2–1.9 cm diam.; pistils (0.9)1.8–4.4 mm long, (0.9)1.3–2.3 mm diam.; ovary 6–9-locular, 1–1.7(3) mm long, 1.3–2.3 mm diam., with sub-basal placentation; locules 1–1.7(3) mm long, 0.2–0.4 mm diam.; ovule sac (0.6)0.8–1.2 mm long; ovules usually 2–4, rarely 5–8 per locule, 1-seriate (2-seriate, if 4 or more ovules), usually contained within translucent, gelatinous ovule sac, sometimes contained within gelatinous matrix (no true envelope), 0.1–0.5 mm long, usually longer than funicle; funicle 0.1–0.3 mm long (can be pulled free to base), sometimes adnate to lower part of partition, style (0.4)0.6–0.8 mm long, (0.8)1.2–1.6 mm diam., similar to style type B; style apex flat to sloping; stigma discoid or subdiscoid, truncate, (0.7)1–1.5 mm diam., (0.1)0.3–0.5 mm high, covering entire style apex, sometimes shallowly depressed at middle; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided to weakly ovate, ca. 1 mm long, 1.6–2 mm diam. at apex; thecae oblong, 0.4–0.6 mm wide, ± parallel to one another, sometimes contiguous; sterile staminate flowers blunt, irregularly 4–6-sided, sometimes clavate or prismatic, 1.4–2.1 mm long, 1.4–2 mm wide. INFRUCTESCENCE pink, green at base with reddish spots outside; berries pale yellowish, rarely orange, with stigmas reddish brown, 7 mm long; seeds 2–3 per locule, drying pale brown to tannish brown, narrowly ellipsoid to oblong-ellipsoid, 1.4–2 mm long, 0.7–0.9 mm diam., with faint striations.

Flowering in *Philodendron sagittifolium* occurs almost throughout the year, principally after the onset of the dry season and continuing throughout much of the rainy season. There is a slight geographical shift, with flowering beginning about one month earlier in Mexico and Guatemala (January through August, less frequently in September and October) and continuing somewhat longer in Panama (February through September, but also rarely in December). Fruits apparently mature in about two months' time, but mature fruits have seldom been collected, only from January and July.

Philodendron sagittifolium ranges from Mexico (Veracruz) to Colombia (and probably also to Venezuela), from sea level to 1800 m elevation. It is probably the most morphologically variable, and one of the most ecologically versatile, species in Central America. In Mexico, this species occurs in "Selva Alta Perennifolia," "Selva Mediana Subperennifolia," "Selva Baja Caducifolia," and "Bosque Caducifolio." In the remainder of Central America, it occurs principally in *Tropical moist forest* and *Premontane wet forest* but also in *Premontane rain forest* and *Tropical wet forest* life zones.

Philodendron sagittifolium is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species, though highly variable in most regards, can be characterized by its appressed-climbing habit; short, stout internodes; sharply two-ribbed, deciduous cataphylls; obtusely flattened, firm petioles usually spotted with violet-purple; and ovate-triangular, moderately coriaceous blades with the posterior rib not at all or only briefly naked along the sinus. Also characteristic is the externally green, frequently purple-spotted spathe, which is reddish purple on the tube within.

In Mexico and Guatemala, *Philodendron sagittifolium* is most easily confused with *P. advena* and *P. purulhense*, differing from both in having the blades somewhat triangular and drying reddish brown rather than generally ovate and drying blackened. See *P. advena* for additional discussion.

In Panama, *P. sagittifolium* may sometimes be confused with *P. annulatum*, which differs in having the petioles somewhat spongy with a purple distal ring, blades typically ovate-oblong, and spathes commonly white on the blade portion. It can be

confused at some stages of development with sterile specimens of *P. bakeri.*

Considering the highly variable nature of this species there are many noteworthy collections, only a few of which can be discussed here.

Whitefoord & Eddy 222 from Panama has the lower blade surfaces drying yellowish brown rather than reddish brown and spathe solid plum-red outside. Also noteworthy is *Hammel et al. 14598,* which reports fruit color to be orange.

A few collections from Puntarenas Province, Costa Rica (*Croat 57243, 67697, Grayum & Hammel 10066*), differ in having the primary lateral veins paler, rather than darker on the lower surface. Sterile specimens from Cocos island (*W. Klawe s.n., Foster 4177*) differ in having the minor veins minutely raised on the upper surface. These specimens may prove to represent distinct species.

A large number of sterile and ostensibly juvenile collections from Nicaragua are of uncertain identity. One series, including *Pipoly 3826, 4055, 5144, Stevens 7628, 12673, 12739,* may ultimately prove to be *P. bakeri.* Two other collections (*Pipoly 5190, 5194*) might prove to be still another species.

Croat 60804, from the coastal cordillera of Venezuela, reported as *P.* cf. *sagittifolium* (Croat & Lambert, 1986) is either this species or a very close relative.

When Regel described *P. sanguineum* Regel, he cited no specimens or country of origin, but Krause (1913) cited a collection he had prepared from the Berlin Botanical Garden of a cultivated Karwinsky collection from Córdoba in Veracruz State, Mexico. While no such collection still exists, Karwinsky collected in Mexico only a few years (1840–1843) before Regel described *P. sanguineum.* Thus it is possible that both Regel and Engler could have been dealing with the same material originally collected by Karwinsky at Córdoba.

Another synonym that deserves mention is *P. lancigerum* Standl. & L. O. Williams, corresponding to a narrow-leaved form of *P. sagittifolium* restricted to the Pacific lowlands of Costa Rica. Epitypification was necessary because the type specimen (*Allen 5612*) consists of only an inflorescence.

Additional specimens examined. BELIZE. **Cayo**: Mountain Pine Ridge, *Bartlett 13052* (MICH); Blancaneaux Lodge, *Wiley 460* (MO); Water Hole, near Vaca, *Gentle 2447* (MICH); Río Ma Cal, San Luis–Cuevas, 1050 ft., *Croat 23497* (MO); 1050 ft., *23539* (MO). **Toledo**: Punta Gorda, *Cosminsky 227* (F); Richardson Creek, lower part, affluent of Bladen Branch, lower part of Maya Mountains, 100–250 m, 88°46–48′W, 16°33′N, *Davidse & Brant 32334* (MO); Columbia road, *Gentle 6118* (LL); San Antonio, *Gentle 5510* (LL); Punta Gorda, *Cosminsky 226* (F); Columbia River Forest Reserve, SW Maya Mountains, trail between Gloria Camp and Edwards Camp to the S, 16°22′N, 89°10′W, *Holst 4499* (MO). COSTA RICA. **Alajuela**: 3 mi. N of San Miguel, 380 m, *Croat 35642* (CR, MO); 8.9 mi. NW of San Ramón, 1100 m, 10°10′30″N, 84°30′W, *Croat 68070* (L, MO); Río Sarapiquí, road to Colonia Virgen del Socorro, 830 m, 10°1′6N, 84°11′W, *Croat 68338* (MO). **Cartago**: Tapantí, ca. 1350 m, 9°47′N, 83°47.5′W, *Grayum 3890* (MO); 1400 m, 9°47′N, 83°48′W, *3322* (K, MO); 31 km S of Siquirres, 850 m, 9°57′N, 83°36′W, *Thompson & Rawlins 1159* (CM); *1160* (CM); 7 km W of Turrialba, *Croat 36829* (MO); Turrialba, Moravia de Chirripó, 1200 m, *Campos & Chavarría 40* (CR, INB); Río Pejibaye, 2 km SW of Taus, 750 m, 9°29′N, 83°41′W, *Lent 2967* (CR, F). **Heredia**: La Selva Field Station, *Hammel 10244* (MO); *Grayum 2306* (MO); *Hammel 9641* (DUKE); La Zona Protectora, SSE of Magsasay, *Schatz 722* (CR, DUKE, MO); 4 mi. N of Vara Blanca, 1350 m, *Croat 35579* (MO). **Limón**: vic. of Moín, 0 m, 10N, 83.04W, *Croat 61206* (MO); Parque Nacional Tortuguero, 2 km S of Tortuguero, 3 m, 10°31′N, 83°30′W, *Robles 2166* (CR, MO); *2178* (CR, MO). **Puntarenas**: Palmar Sur–Piedras Blancas, 20 m, *Croat 32917* (MO); Quebrada Aparicio–Quebrada Aguabuena, Rincón de Osa, 200–400 m, 8°42′N, 83°31′W, *Grayum et al. 4017* (CR, MO); Rincón de Osa, region to W of airstrip, 40–100 m, *Utley & Utley 1119* (F); San Vito de Coto Brus–Ciudad Neily, 300–600 m, 8°41′N, 82°56.5′W, *Hammel 14159* (CR, MO); El Campo, Aguabena, 350 m, 8°42′50″N, 83°31′42″W, *Herrera 3959* (INB, MO); Las Brisas–Las Juntas de Coto Brus, ca. 900 m, 8°52′N, 82°57′W, *Grayum & Hammel 5692* (INB, MO); Parque Nacional Corcovado, Sirena, 1–10 m, 8°28′N, 83°35′W, *Kernan & Phillips 1028* (MO); 1–50 m, *Kernan & Phillips 1089* (MO); *Kernan 461* (CR, MO), *574* (CR, MO); 10 m, *Aguilar 3396* (INB); Río Claro, 5 m, *Kernan 783* (CR, MO); Las Cruces Botanical Garden–Río Jaba, ca. 3 km SW of San Vito de Coto Brus, ca. 1050–1200 m, 8°47′N, 82°58′W, *Grayum 5624* (CM, CR, INB, MEXU, MO, U); San Vito de Java, ca. 4000 ft., *Croat 32904* (MO); 1 mi. S of San Vito de Java, ca. 3500 ft., *Raven 21882* (BM, DS, F); 6 km S of San Vito de Java, 4000 ft., *Raven 22009* (DS, F, WIS); Las Cruces Botanical Garden, ca. 1300 m, *Croat 44440* (MO); Golfito, near TV transmission tower, 2000 ft., 8°49′N, 82°58′W, *Croat 57243* (MO), *57231* (MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1150 m, *Croat 22287* (F, MO), *22257* (MO); hills above Palmar Norte, 100–200 m, *Croat 35141* (MO); Punta Catedral, ca. 7 km SE of Quepos, 20–70 m, 9°22.5′N, 84°09′W, *Grayum & Sleeper 5903* (MO); Punta Quepos (3 km S of Puerto Quepos), 0 m, 9°24′N, 84°10′W, *Grayum 6613* (CR, MO, PMA, US); road to Rincón de Osa, 16.5 km W of Inter-American Highway, 280 m, 8°45′N, 83°22′W, *Grayum et al. 7550* (INB, MO); Reserva Forestal Golfo Dulce, S of Rincón de Osa, 150 m, 8°37′N, 83°28′W, *Hammel & Robles 16728* (CR, MO); 150–200 m, *16759* (CR, MO); 450 m, *G. Herrera 3953* (CR, INB); ca. 0.7 km N of Golfito–Villa Briceño road, 160–260 m, 8°40′30″N, 83°12′W, *Grayum & Hammel 10066* (CR, MO); Cantón de Golfito, Jiménez, Alto de la Carbonera, road to Cerro de Osa, 200–350 m, 8°25′30″N, 83°19′W, *A. Chacón 1069* (CR, INB, MO); 3.1 mi. NW of center of Golfito, 30 m, 8°11′N, 83°12′W, *Croat 67632* (CM, CR, MEXU, MO, WIS); Piedras Blancas–Rincón Road, Mile 3.7, 90–105 m, *Croat 67697* (CR, MO); Cocos Island, valley behind Bahía Iglesias, *Foster 4177* (F, MO); *Klawe s.n.* (POM). **San José**: San Isidro de El General–Dominical, SW of San Isidro.

4.8 mi. from Río Pacuare, 1000 m, *Croat 35254* (MO); 9 mi. SW of Río Pacuare, 680 m, *35343* (MO); ca. 0.5 mi. above turnoff to Canaán at Rivas, 900 m, *Croat 43430* (CR, MO); *43415* (MO); Estación Carrillo, Fila Cañon del Río Sucio 450–700 m, *A. Chacón & Herrera 1705* (CR, MO); Carara–El Sur de Turrubares, 200–310 m, 9°45′15″N, 84°31′30″W, *Grayum 10451* (CR, INB, MO); Z. P. La Cangreja, Santa Rosa de puriscal, 400 m, 9°42′50″N, 84°23′30″W, *Morales 1468* (CR, MO); Acosta, Valle del Candelaria, 1000–1050 m, *Morales & González 4581* (CR, INB); Tarrazu, vic. Hormiguero, 1100–1200 m, *Croat 78938* (INB, MO); *78959* (CR, INB, MO); 990–1100 m, *Croat & Hannon 79110* (MO); Parque Nacional, sector Esquinas, vic. Fila Gamba, 200–300 m, *Croat & Hannon 79294* (INB, MO). GUATEMALA. Eastern portions of Verapaz and Chiquimula, *Watson 106* (GH). **Alta Verapaz**: E of Tactic, 1300 m, *Steyermark 43993* (F, US); near Chirriacté, on the Petén Highway, ca. 900 m, *Standley 92189* (F); Chapultepec Farm, 62 km from Cobán on Sebol Road, *Contreras 4823* (LL); Río Carchá, Cobán–San Pedro Carchá, ca. 1360 m, *Standley 89891* (F). **Baja Verapaz**: Mpio. Purulhá, El Progreso–Cobán, Hwy. CA-14, 17 mi. N of junction with Hwy. 17, 1620–1720 m, 15°13′N, 90°12′W, *Croat & Hannon 63766* (CAS, CR, EAP, MO, SAR, USCG). **Chimaltenango**: Quisaché, 1800 m, *Standley 62029* (F). **Izabal**: Escobas–Santo Tomás, Santo Tomás Bay, 0–2 m, *Steyermark 39331* (F); between Milla 49.5 and ridge 6 mi. from Izabal, Montaña del Mico, 65–600 m, *Steyermark 38506* (F, US); vic. EXMIBAL Camp 2 (La Gloria), NW of Lake Izabal, 400–500 m, *Jones & Facey 3283* (NY); Sierra de las Minas, 13 km E of Doña María, 240 m, ca. 15°14′N, 89°20′W, *Harmon & Fuentes 5857* (UMO); Río Frío, 75–150 m, *Steyermark 41533* (F, LL). **Petén**: Canchacan, near San Luis, *Lundell 16325* (LL); Dolores, 300 m, *Contreras 2562* (LL). **Quezaltenango**: La Shuya, SW of San Martín Chile Verde, ca. 1620 m, *Standley 67882* (F). HONDURAS. Mont. de la Flor., 3300 ft., *von Hagen & von Hagen 1304* (F, NY). **Atlántida**: Quebrada Grande, ca. 10 km SW of La Ceiba, 80–200 m, 15°42′N, 86°51′W, *Liesner & Mejía 26011* (MO); *26352* (MO); 80–180 m, 15°42′N, 86°51′W, *Liesner 26179* (MO). **Comayagua**: El Achote, above Siguatepeque, 1350 m, *Yuncker et al. 5894* (F, GH, K, MO, NY, U). **El Paraiso**: El Junquillo–El Robledal, Sierra el Chile, 1300 m, *Molina 14142* (EAP, F, NY). **Olancho**: Catacamas–La Presa, N of Catacamas, 500–600 m, *Standley 18698* (EAP); *Nelson 9875* (TEFH, US); Río Olancho, San Esteban–Bonito Oriental, 14.8 mi. NE of San Esteban, 635 m, 15°25′N, 85°47′W, *Croat & Hannon 64405* (DUKE, LL, MO); San Francisco de la Paz–Gualaco, 7.3 mi. NE of San Francisco de la Paz, 1130 m, 14°58′N, 86°12′W, *Croat & Hannon 64197* (B, BM, CM, MICH, MO, NY, QCA); 13.6 mi. SW of Gualaco, 1300 m, 15°N, 86°07′W, *Croat & Hannon 64295* (F, K, MO, NY); Mpio. La Unión, 6 mi. E of La Unión along road to Olanchito, 950 m, 15°03′N, 86°35′W, *Davidse et al. 35428* (MO). **Yoro**: Cordillera Nombre de Dios, El Guaymon–San José de Texíguat, Cerro Aguacatales, 830 m, 15°29′N, 87°37′W, *Davidse et al. 34524* (EAD, MO, TEFM); *34524* (EAD, MO, TEFM); Río Pijol Valley, 6–7 km S of Nueva Esperanza, 1570–1670 m, 15°12′N, 87°35′W, *Liesner 26581* (MO). MEXICO. Patria, *Engler 198* (GH, P). **Chiapas**: Mpio. Ocosingo, 16 km NW of Boca Lacantún, 900 m, *Martínez 21345* (MEXU, MO); 12 km N of Monte Líbano, 950 m, *Martínez 21252* (MEXU, MO); Cascada Corralita, SW of Ocosingo, 600 m, 16°59′N, 92°08′W, *Hammel et al. 15677* (MO); Palenque–Bonampak, 69 mi. SW of Palenque, 450 m, *Croat 40197* (F, MO), 6 mi. N of Ocozocoautla, 1000 m, *Croat 40581* (B, MEXU, MO); Palenque–Ocosingo, Hwy. 199, 43 mi. SW of Palenque, 810 m, *Croat 40337* (MO); 13 mi. N of Ocozocoautla, 900 m, *Croat 40632* (MO); San Cristóbal de Las Casas–Palenque, Villa Paraíso, 136 km NE of San Cristóbal, 450 m, 17°29′N, 92°05′W, *Hammel et al. 15641* (MO); 18–20 km N of Ocozocoautla, 800 m, *Breedlove 25202* (DS); 3 mi. N of Pueblo Nuevo Solistahuacán, 1700 m, *Breedlove & Smith 32436* (DS); 6700 ft., *Thorne & Lathrop 40267* (RSA). **Morelos**: Cuernavaca, Barranca del Salto de San Antonio, *Moore & Bunting 8823* (BH); Iturbide, *Bourgeau 1417* (K, P). **Oaxaca**: Latani, Dtto. Choapam, 900 m, 17°24′N, 95°48′W, *Schultes & Reko 900* (ECON, GH); Sierra de Juárez, Tuxtepec–Oaxaca, Highway 67, 6–14 mi. above bridge at Valle Nacional, ca. 580 m, *Moore & Bunting 8902* (BH, CM); *8892* (BH); 660 m, *Croat 39752* (MO); *39757* (MO); *43917* (CM, MO); 1400 m, *Croat 48000* (L, MEXU, MO); 705 m, 17°44′N, 96°19′W, *Croat & Hannon 65537* (B, MO); 55 km S of Tuxtepec, 630 m, 17°37′N, 96°20′ W, *Hammel & Merello 15482* (MO, NY); Uxpanapa region, Esmeralda–Río Verde, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63237* (CR, MO, VEN); *63299* (MO); Palomares–Matías Romero, road to Uxpanapa, 44 km E of entrance at Sarabia, on Rte. 185, 125 m, 17°09′N, 94°37′W, *Hammel & Merello 15556* (MO); *15555* (MO); Uxpanapa, 14 km E of Campamento La Laguna (Poblado D.S.), 150 m, 17°05′N, 94°35′W, *Hammel & Merello 15578* (MO); Río Uxpanapa, *Matuda 38666* (MEXU); Ixtlán, Mpio. Comaltepec, Puerto Antonio, ca. 1300 m, 17°45′N, 96°30′W, *Luna 436* (MO); Highway 175, 1 km above Vista Hermosa, 1255 m, 17°35′N, 96°21′W, *Boyle & Boyle 684* (MO). **Veracruz**: Conejo–Huatusco, Hacienda El Mirador vicinity, km 45 on highway, *Moore & Bunting 8862* (BH, MO); *8863* (BH, MO); El Mirador, *8857* (BH, MO); Fortín de las Flores (Posada Loma), 850 m, *Nevling & Gómez-Pompa 287* (cultivated, XAL); Catemaco–Acayucan, ca. 8 mi. S of Catemaco, near Zapoapan, ca. 400 m, *Moore & Bunting 8925* (BH); Fortín, Cervecería Moctezuma, 1000–1150 m, *Croat 39415* (CM, F, MO); 900 m, *Croat 44038* (MO); 5.7–6 mi. from Catemaco, road to Sontecomapan, ca. 380 m, *Moore & Bunting 8941* (BH); Playa Montepío, 0 m, 18°38′N, 95°05′W, *Hammel & Merello 15498* (BR, CM, MO); Coatzacoalcos River, Fortuño, 30–50 m, *Williams 8702* (F); Estación de Biología Trioucak "Los Tuxtlas," ca. 31 km by road N of Catemaco, along road to Montepío, 250–300 m, 18°60′N, 95°07′W, *Grayum & Sleeper 8355* (MO); 300 m, 18°44′N, 85°10′W, *Hammel & Merello 15490* (CM, MO); 170–200 m, *Gentry et al. 32488* (MO); 250 m, *Ibarra 589* (MO); Mpio. Coatepec, Tuzamapan–Jalcomulco, Cerro de Achichuca, 700 m, 19°23′N, 96°48′W, *Castillo & Tapia 678* (F, MO); Mpio. Hidalgotitlán, toward La Laguna, 160 m, 17°16.6′N, 94°33.4′W, *Valdivia 744* (XAL); Hidalgotitlán, 150 m, *Valdivia 1351* (XAL); near La Escuadra, 160 m, 17°19′N, 94°38.5′W, *Valdivia 1330* (XAL); Mpio. J. de Ferrer, Cerro de Villa Rica, near Plan de la Flor, 1250 m, 19°48′N, 96°46′W, *Castillo et al. 1715* (F); Mpio. Jesús Carranza, 2 km N del Poblado 2, Ejido F. J. Mina, 120 m, 17°16′N, 94°40′W, *Vásquez & Navarrete 2383* (MO); Mpio. Pajapan, Volcán San Martín Pajapan, 6 km NW of Pajapan, 1200 m, 18°18′20″N, 94°43′30″W, *Nee et al. 24974* (F, MO); Sontecomapan–Montepío, N of San Andrés Tuxtla, 150–200 m, 18°42′N, 95°10′W, *Croat & Hannon 63158* (MO, NY, US); Mpio. Tlapacoyan, Río Tablazos, Tlapacoyan–Altotonga, 6 km SSW of Tlapacoyan, 19°56′N, 97°13′W, *Nee et al. 26090*

(F, MO, NY); Vallé de Córdova, *Bourgeau 2296* (K, P). NICARAGUA. **Estelí**: El Zacatón (Plan Helado), ca. 1300 m, 13°13′N, 86°14′W, *Moreno 17521* (MO); Laguna de Miraflores, ca. 1200 m, *Grijalva 952* (MO). **Jinotega**: ca. 5–8 mi. SW of Jinotega, 1500 m, *Croat 43084* (CM, MO); San Ramón–Paricutín, Comarca Kilambé, SE of Cerro Kilambé, 800–900 m, 13°35′N, 85°40′W, *Moreno 7687* (MO); along Hwy. 3 ca. 1 km NW of La Fundadora entrance, 1450–1520 m, 13°01′N, 85°56′W, *Stevens & Henrich 20435* (MO), Las Camelias–La Salvadora, 1100–1150 m, 13°05–06′N, 85°53–54′W, *Stevens et al. 15327* (MO); N slope of Volcán Yalí, 1200–1400 m, 13°15′N, 86°10′W, *Stevens et al. 15091* (MO); Matagalpa–Jinotega Road, Km 146, 1200–1400 m, *Moreno 571* (MO); Laguna Miraflores, ca. 26.1 km NE of Hwy. 1 at Estelí, 1250–1300 m, ca. 13°15′N, 86°15′W, *Henrich & Stevens 243* (MO); Las Camelias–La Salvadora, road from Hwy. 3 through La Fundadora, 1100–1150 m, ca. 13°05–06′N, 85°53–54′W, *Stevens & Grijalva 15322* (MO); Macizos de Peñas Blancas, vic. of Finca of Manuel Estrada (El Cielo), 1200–1400 m, ca. 13°15′N, 85°41′W, *Stevens 11665* (MO); 1500–1650 m, ca. 13°15–16′N, 85°41′W, *Stevens 11430* (MO); Río Bocay, Salto Kayaska, 190–340 m, ca. 13°51′N, 85°22′W, *Stevens et al. 16479* (MO). **Matagalpa**: Valle de Arenal, on road to Sanatorio de Aranjuez, 1400 m, 13°02′N, 85°55′W, *Davidse et al. 30444* (MO); 13°01′N, 85°54′W, *Moreno 9583* (MO); Fuente Pura, km 142, 1400–1450 m, 13°N, 85°55′W, *Moreno 17017* (MO); road to Cerro La Carlota, 2 km from Tuma, 1040–1100 m, 12°58′N, 85°52′W, *Moreno 15659* (MO); Cerro Picacho, behind La Selva Negra Hotel, 1200–1540 m, 13°N, 85°55′W, *Davidse et al. 30311* (MO). **Nueva Segovia**: Río San Fernando Valley, Cerro El Peñascal, 800–1125 m, 13°2–3′N, 86°19–20′W, *Stevens 3297* (BM, MO). **Río San Juan**: Bocas de Sábalo, 70–100 m, 11°03′N, 84°27′W, *Moreno 26692* (MO). **Zelaya**: El Empalme–Limbaika, junction of road to Alamikamba, ca. 25 m, ca. 13°32′N, 84°30′W, *Stevens 12739* (MO); road to Mina Nueva América, ca. 10 km N of main road, *Stevens 12673* (MO); ca. 11.3 km N of main road, *Pipoly 5283* (MO); ca. 6.3 km S of bridge at Colonia Yolania, ca. 200–300 m, ca. 11°36–37′N, 84°22′W, *Stevens 4824* (MO); Cerro El Hormiguero, W range, ca. 1100–1183 m, ca. 13°44′N, 85°W, *Pipoly 5198* (MO); *5194* (MO); *5190* (MO); Cerro La Pimienta number 1, ca. 900–980 m, ca. 13°45′N, 84°59′W, *5107* (MO); *5114* (MO); ca. 13 km above Kururia, on road to San Jerónimo, <200 m, *Pipoly 3826* (MO); 1 km S of Monkey Point, ca. 5 m, 11°35′N, 83°39′W, *Moreno & Sandino 12531* (MO); Monkey Point, 1.5 km NW, 1–5 m, 11°36′N, 83°38′W, *Moreno & Sandino 11957* (MO); Río Kisalaya, near Tala Has and Puente Mango, 40–60 m, ca. 14°41′N, 84°03′W, *Stevens 7628* (BM, MO); Río Mico, near El Recreo, ca. 30 m, *Standley 19404* (F); *19525* (EAP, F), *19614* (F); Río Pis Pis, 0.5–1.5 km from Plantel El Salto, road to Bonanza, ca. 140 m, ca. 14°03′N, 84°37′W, *Stevens 18871* (MO); Río Punta Gorda, Atlanta, ca. 10 m, 11°34′N, 84°01′W, *Moreno & Sandino 12770* (MO); Waspam–Puerto Cabezas, Río Troncera, <200 m, ca. 14°43′N, 84°06′W, *Pipoly 4055* (MO). PANAMA. **Bocas del Toro**: Gualaca–Chiriquí Grande, 4.2 mi. E of Chiriquí Grande, ca. 0 m, 8°55′N, 82°09′W, *Croat 66814* (MO); 0.4 mi. SE of Punta Peña, 120 m, 8°57′N, 8°56′W, *Croat 74939* (AAU, CR, MO, NY); Fortuna Dam area, N of Fortuna Dam, 650–700 m, 8°45′N, 82°15′W, *McPherson 11131* (MO); Chiriquí Grande–Fortuna, 1.6 mi. N of Continental Divide, 770–790 m, 8°45′N, 82°17′W, *Croat & Zhu 76453A* (MO), *76456A* (CM, MO); 10 mi. N Divide, 1 mi. N from highway, 130 m, 8°46′N, 82°11′W, *Hammel et al. 14598* (MO); 4.3 km N of Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60210* (CM, MO); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60259* (CAS, CR, F, KYO, M, MEXU, MO, PMA). **Canal Area**: Frijoles–Monte Lirio, 30 m, *Killip 12133* (US); hills N of Frijoles, *Standley 27598* (US); Pipeline Road, 14 mi. NW of Gamboa gate, *Croat 12363* (MO); Barro Colorado Island, *Croat 6472* (F, MO, RSA, SCZ); *Aviles 25* (F); *46* (F); Gatún Lake, *Standley 31398* (US); *Croat 6531* (F, MO, SCZ), *6334* (MO), *5052* (MO), *10901* (MO), *8290* (MO), *10859* (MO), *9018* (MO), *8999* (MO), *10076* (MO); *Silvestre s.n.* (MO); *Croat 6023* (MO); Summit Gardens, *Croat 59139* (MO), *17155* (MO), *10768* (MO), *17060A* (MO). **Chiriquí**: Finca Ojo de Agua, 1300 m, 8°51′N, 82°46′W, *Knapp 1590* (MO); Cañas Gordas–Volcán, 1 m E of Cañas Gordas, ca. 1000 m, *Croat 22304* (MO); 8 mi. W of Puerto Armuelles, in vic. of San Bartolo Límite, ca. 600 m, *Croat 22022* (MO), *22026* (MO); Cerro Colorado, above San Félix, 15–18 mi. N of Pan-American Highway, 800–1000 m, *Croat 33179* (CM, MO); Gualaca–Chiriquí Grande, Fortuna Dam area, 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *Croat 67843* (CM, MO); 5.9 mi. NW of Los Planes de Hornito, 1225 m, 8°45′N, 82°14′W, *Croat 67795* (CR, MO, PMA); 1400 m, *Croat 48719* (MO); *48697* (MO); *48681* (MO); Gualaca–Chiriquí Grande, 8 mi. beyond Los Planes de Hornito, trail to Río Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67918* (CAS, COL, L, MEXU, MO, PMA, US); 10.1 mi. NW of Los Planes de Hornito, 1250 m, 82°17′W, 8°45′N, *Croat 50040* (CM, MO); Quebrada Los Chorros–Quebrada Honda, N of Fortuna Lake, 1100 m, 8°45′N, 82°14′W, *Churchill & Churchill 6107* (MO); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60056* (B, CAS, F, L, MBM, MO, P, PMA); Cerro Colorado, 2.3 km above Chame, 1000 m, *Croat 37067* (MO). **Coclé**: Penonomé–Coclecito, Río Cascajal, 5.7 mi. N of Llano Grande, 210 m, 8°40′N, 80°26′W, *Croat 67541* (CR, MO); El Copé region, 9.4 km above El Copé, 750–900 m, *Croat 44726* (MO); Alto Calvario, 710–800 m, *Croat 68716* (EAP, G, HNMN, MO, TEX); 8°39′N, 80°36′W, *68849* (MO); 580–740 m, 8°38′N, 80°36′W, *Croat 67522* (MO, US); El Valle region, La Mesa, above El Valle de Antón, 860–900 m, *Croat 37407* (MO); 870 m, 8°50′N, 80°07′W, *Hoover 1320* (MO); 800–900 m, 8°38′N, 80°09′W, *Croat 67152* (B, CAS, CM, COL, DUKE, F, K, L, MEXU, MO, NY, PMA, QCA, TEX, VDB, WIS); 800 m, 8°36′N, 80°07′W, *Croat & Zhu 76691* (MO); Cerro Gaital, *Churchill 3907* (MO). **Colón**: Sabanitas–Portobelo, Río Piedras Lumber Road, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75159* (MO); Río Indio–Miguel de la Borda, 0 m, *Croat 36906* (MO); Miguel de la Borda, *Croat 9856* (F, MO, RSA, US); Santa Rita Ridge Road, 10.6 km from highway, ca. 380 m, *Croat 34345* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76964* (MO); along Río Guanche ca. 2 km E of bridge on the main Puerto Pilón–Portobelo Road, 100 m, 9°30′N, 79°39′W, *Croat 75176* (MO). **Darién**: Cerro Pirre region, middle slopes on W side, 550–760 m, 7°57′N, 77°46′W, *Croat 68958* (MO); *68893* (MO); Río Cana–Río Escucha Ruido, above Cana Gold Mine, 1310–1430 m, *Croat 37755* (MO); *37818* (MO); *37827* (MO); S of El Real, Alturas de Nique, near Cana mine, along old Camino Real toward Colombia, 800–1000 m, 7°45′N, 77°40′W, *McPherson 11536* (MO); Río Cocalito, ca. 5 mi. from P. Cocalito, *Whitefoord & Eddy 222* (BM, MO); Parque Nacional del Darién, Panama–Colombia border, Río Pucuro, Cerro Tacarcuna, ca. 6

km N of Cerro Mali, 1300–1500 m, 8°09.5′N, 77°15′W, *Hammel et al. 16537* (MO, PMA). **Herrera**: Las Minas, Primer Ciclo de Chepo, 900 m, 7°43′N, 80°50′W, *Galdames et al. 1765* (MO); 18 km W of Las Minas, Alto Higo, N slope, 2400 ft., *Hammel 4227* (MO). **Los Santos**: Azuero Peninsula, Jobero–Río Pedregal, 300–700 m, *Croat 34479* (MO); Río Guanico valley, 600 m, 7°18′N, 80°30′W, *McPherson 9245* (MO, NY, SCZ). **Panamá**: Cerro Azul, *Croat 17281* (MO); El Llano–Cartí Road, ca. 16–18 km N of Pan-American Highway, 400 m, *Tyson & Nee 7352* (MO); Mile 5–9, 200–250 m, 9°15–16′N, 78°59′N, *Thompson 4624* (CM); Mile 10, 330 m, *Croat 33823* (CM, F, MO, TEX, WIS); Mile 7, 460 m, *75109* (MO); Km 7–12, 360–400 m, *25096* (MO); Mile 8.2, 450 m, 9°14′N, 79°W, *Knapp & Hufi 4412* (MO); Mile 12, 200–500 m, *Liesner 695* (MO); Mile 5–9, 200–250 m, 9°15–16′N, 78°59′W, *Thompson 4636* (CM); Cerro Campana, 800 m, 8°41′N, 79°56′W, *Croat 74770* (AAU, MO); *74771* (MO, PMA); *17177* (MO); ca. 850 m, 8°40′N, 79°50′W, *Thompson 4577* (CM); 700 m, 79°55′W, 8°40′N, *Hamilton et al. 1174* (MO); *Hammel 5561* (MO); ca. 1 mi. from Inter-American Highway, ca. 150 m, *Croat 35983* (MO); *12063* (MO); 800 m, 8°41′N, 79°56′W, *74770* (MO); Cerro Jefe region, near summit 750–800 m, 9°14′N, 79°22′W, *Croat 67087* (F, MO); 800–1000 m, *Gentry 2892* (GH, MO); 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76608* (CR, GB, MBM, MEXU, MO, NY); 4.6 km beyond peak, on road to Altos de Pacora, 26.3 km from highway, ca. 600 m, *Croat 35933* (MO); 3–3.5 mi. NE of Altos de Pacora, 11.1–11.6 mi. beyond Lago Cerro Azul, 700–750 m, 9°15′N, 79°25′W, *Croat 68695* (MO, PMA). **San Blas**: beach E of Puerto Obaldía, *Croat 16910* (MO); *16911* (MO); *16914* (MO); 7 mi. N of Inter-American Highway, 550 m, 9°43′N, 78°68′W, *Croat 60506* (MO); Cerro Brewster, 800–850 m, 9°18′N, 79°16′W, *de Nevers et al. 6287* (MO); El Llano–Cartí Road, vic. Nusagandi, 450 m, 9°18′N, 79°59′W, *Croat 75150* (CM, MO, PMA); 350 m, 9°20′N, 79°W, *Croat & Zhu 77012* (CM, MO). **Veraguas**: Dist. Montijo, Isla de Coiba, 7°37′N, 81°44′W, *Galdames et al. 2213* (PMA); *2073* (CM, MO, PMA); 400 ft., *Antonio 2383* (MO); *2343* (MO, PMA); 400 m, 7°31′N, 81°51′W, *Galdames et al. 2284* (MO, PMA); 50 m, 7°35′N, 81°47′W, *Galdames 2256* (MO, PMA); Santa Fe region, 7 km W of Santa Fe, 2900 ft., *Nee 11192* (MO, RSA); Cerro Tute, to 1200 m, *Witherspoon et al. 8873* (MO); Santa Fe–Río San Luis, at Río Segundo Brazo, 480 m, 8°33′N, 81°08′W, *Croat 66886* (MO, PMA); *66916* (MO, PMA), *66920* (MO).

Philodendron scalarinerve Croat & Grayum, sp. nov. TYPE: Panama. Panamá: road past and 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-American Hwy., 11.1–11.6 mi. beyond Lago Cerro Azul, 700–750 m, 9°15′N, 79°25′W, *Croat 68692* (holotype, MO–3585744; isotypes, B, CAS, COL, CR, F, K, NY, PMA, US). Figures 357–363.

Planta hemiepiphytica; internodia 1–1.5(3) cm longa, 1.5–3.5(4) cm diam.; cataphylla usque 22 cm longa, incostata vel obtuse 1-costata, raro acute 2-costata, persistentia semi-intacta; petiolus subteres, 20–75 cm longus, 0.7–1.5 cm diam.; lamina oblong-elliptica vel leniter cordata, 33–67 cm longa, 11.4–40 cm lata, cum nervis conspicue scalariformibus inter nervos minores; inflorescentia 1–4; pedunculus 6–20 cm longus, subteres; spatha 16–21.5 cm longa, pallide viridis; lamina spathae seminitida, extus striata alba apice, intus viridi diluta; tubo spathae hebetato, extus striato albo basi, intus viridalbo; pistilla 4–6(7–8)-locularia; loculi (10)12–14-ovulati.

Appressed-climbing hemiepiphyte; stems moderately short; leaf scars conspicuous, 2–4 cm wide; internodes 1–1.5(3) cm long, 1.5–3.5(4) cm diam., about as long as broad; roots moderately few per node, short, drying dark brown, matte, longitudinally ridged; cataphylls moderately thick, to 22 cm long, unribbed to bluntly 1-ribbed, rarely sharply 2-ribbed, drying dark brown, persisting semi-intact, eventually fibrous at upper nodes. LEAVES erect-spreading, clustered at or near stem apex; **petioles** 20–75 cm long, 0.7–1.5 cm diam., subterete, stiff, green, obtusely flattened, sulcate adaxially; sheathing 1–2.5 cm long; geniculum scarcely thicker than petiole, 6–7.8 cm long slightly paler than petiole; **blades** oblong-elliptic to narrowly ovate, moderately coriaceous, acuminate at apex (the acumen sometimes inrolled, to 2 mm long), obtuse to subcordate at base, 33–67 cm long, 11.4–40 cm wide (1.2–4 times longer than wide), (0.82–2.11 times longer than petiole), broadest at the middle, margins weakly undulate, upper surface dark green, semiglossy, lower surface much paler, matte to semiglossy, obscurely dark-punctate at 10× magnification; midrib convex to narrowly raised, sometimes paler than surface above, convex to thicker than broad and concolorous below; basal veins 1–4 per side, with all free to base; primary lateral veins 5–18 per side, departing midrib at a 60–75° angle, arcuate-ascending to the margins, sunken above; minor veins arising from the midrib only; with scalariform "cross-veins" weakly visible when fresh, conspicuously raised above on drying, barely visible below. INFLORESCENCES spreading, pendent, shorter than leaves, 1–4 per axil; peduncle 6–20 cm long, subterete, white-streaked near apex, spongy; **spathe** 16–21.5 cm long (0.6–1.4 times longer than peduncle), pale green, acuminate at apex, obtuse at base, convolute to about the middle at anthesis; spathe blade semiglossy, white-streaked at apex outside, light green inside; spathe tube matte, white-streaked at base outside, 5–7 cm long, 2–3.5 cm diam., greenish white inside; **spadix** sessile, erect, (7.6)9–12 cm long, broadest at the base or at the middle or below the middle; pistillate portion light green, slightly tapered above middle or toward both ends, (1.7)2.6–4.3(7.8) cm long, 0.8–1.3 cm diam. at apex, 0.8–1.4 cm diam. at middle, 0.9–1.4 cm wide at base; staminate portion 4.8–8.7 cm long; fertile staminate portion (9)12 mm diam. at base, (9)12 mm diam. at middle, (6)10 mm diam.

ca. 1 cm from apex, broadest at the base, slightly narrower than the pistillate portion, slightly narrower than the sterile portion; sterile staminate portion as broad as the pistillate portion, 1.2–1.4 cm diam.; pistils (1.4)2.3–2.8(3.2) mm long, (1)1.4–1.9 mm diam.; ovary 4–6(7–8)-locular, (0.7)1.5–1.8(3) mm long, (1.1)1.5–1.9 mm diam., with axile placentation; locules (0.7)1.5–1.8(3) mm long, 0.4–0.6 mm diam.; ovules (10)12–14 per locule, 2-seriate, (0.1)0.3–0.4 mm long, longer than funicle; funicle 0.1–0.2(0.3) mm long, adnate to lower part of partition, style 0.5(0.7) mm long, 1.1–1.4(2.2) mm diam., similar to style type B; style apex usually flat, sometimes rounded or domed, with stigma lobes over depressions (if apex is flat or domed); stigma usually lobed, sometimes subdiscoid or truncate, lobed, 0.9–1.2(1.4–1.7) mm diam., (0.1)0.2–0.3 mm high, covering entire style apex, inserted on center of style apex, sometimes medially depressed; the androecium truncate, prismatic, sometimes weakly oblong to oblong, margins 4–6-sided, sometimes scalloped, (0.6)0.8–1.1 mm long, 1–1.8 mm diam. at apex; thecae oblong, 0.3–0.5 mm wide, ± parallel to one another, contiguous or nearly contiguous; pollen ellipsoidal, <0.1 mm long, <0.1 mm diam.; sterile staminate flowers irregularly 4–6-sided, clavate or weakly rounded, blunt, rarely irregularly 3–5-sided or depressed with a furrow, (0.8–1.2)1.7 mm long, 0.9–1.5(1.5–2 mm) wide.

Flowering in *Philodendron scalarinerve* occurs principally in the early rainy season (June through August) but also in March. Post-anthesis inflorescences have been collected primarily from June through September, but one such Costa Rican collection was made in January and one South American collection in December. Immature fruiting collections are known from July through December.

Philodendron scalarinerve ranges from Costa Rica to Ecuador, from sea level to 1325 m in *Tropical wet forest, Premontane rain forest, Tropical Lower Montane rain forest,* and *Tropical rain forest* (Colombia).

Philodendron scalarinerve is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its short internodes, bluntly 1-ribbed to unribbed cataphylls persisting as pale fibers with small fragments of thin, pale epidermis, terete to subterete petioles, narrowly ovate to oblong-ovate blades drying dark with the "cross-veins" (tertiary veins that extend between the minor veins) numerous and conspicuous on both surfaces and uniformly greenish spathes.

Additional specimens examined. COSTA RICA. **Heredia**: Finca El Bejuco, N of Río Sarapiquí, Chilamate de Sarapiquí, ca. 100 m, 10°27′N, 84°04′W, *Grayum & Ray 5564* (CR, MO); Cerros Sardinal, ca. 2–2.5 km N of Chilamate de Sarapiquí, 80–160 m, 10°28′N, 84°04′W, *Grayum et al. 6147* (CR, MO). **Limón**: Cerro Coronel, S of Río Colorado, 10–80 m, 10°40′30″N, 83°39′30″W, *Davidse & Herrera 31475* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60173* (CM, MO); 3.2 mi. N of Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60251* (MO, NY, PMA, QCA). **Chiriquí**: Fortuna Lake area, Río Chiriquí Valley, vic. IRHE facilities, 1100–1200 m, 8°45′N, 82°18′W, *Croat 66593* (AAU, CAS, CM, COL, DUKE, G, GH, HUA, K, L, MEXU, MO, NY, PMA, QCA, TEX, US, VDB, VEN); Lago Fortuna, along trail to Río Hornito, 8°45′N, 82°18′W, *Croat & Zhu 76419* (MEXU, MO, SCZ, US). **Coclé**: El Copé region, 5–6 mi. N of El Copé, 600–800 m, 8°38′N, 8°35′W, *Croat & Zhu 77222* (HUA, MO, MY, QCNE); ca. 0.5 mi. N of Continental Divide at Alto Calvario, ca. 5.5 mi. N of El Copé, 800 m, 8°39′N, 80°36′W, *Croat 75081* (MO, US); Alto Calvario, ca. 6 km N of El Copé, 710–800 m, 8°39′N, 80°36′W, *Croat 68723* (MO, PMA, RSA); 720–800 m, 8°38′N, 80°35′W, *McPherson 12856* (BR, CAS, CR, MO, PMA); 930 m, *Croat 49196* (CAS, L, MO); *49174* (MO), *49154* (MO); *68722* (DUKE, F, MO, PMA); 750–900 m, *44737* (CM, MO); *44720* (MO, PMA); El Valle region, La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *Croat 67203* (CR, MO, PMA, QCA, US); *25436* (F, MO); 880 m, *37569* (F, MO); ca. 1000 m, *Kennedy & Dressler 1759* (MO); *Luteyn & Kennedy 1717* (DUKE); Cerro Gaital, 800–900 m, 8°37′N, 80°07′W, *McPherson 11196* (MO, PMA). **Colón**: Santa Rita Ridge Road, ca. 22 km from Highway, 500 m, 9°25′N, 79°40′W, *Hammel et al. 14478* (MO). **Panamá**: Vertiente Pacifica, 150–200 m, 9°13.5′N, 78°15′W, *Herrera 1604* (K, MO, PMA, STRI, US); Cerro Jefe region, 26.3 km from highway, ca. 600 m, *Croat 35919* (MO); Campo Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Croat 22701A* (CM, MO, NY); 700 m, *Croat 27072* (F, MO), *27093* (MO); ca. 1 mi. beyond Alto de Pacora, 2600 ft., *Hammel & Kress 13420* (DUKE); El Llano–Cartí, 5–6 mi. N of Inter-American Highway at El Llano, 350–375 m, *Croat 34805A* (F, MO, NY, QCA, WIS); Mile 6.8, 350 m, *Croat 49112* (MO); Mile 7, 9°19′N, 79°59′W, *Croat 75103* (CM, MO). **San Blas**: Nusagandi, 300 m, 9°15′N, 79°W, *McPherson 11066* (MO, PMA); Río Urgandi–Cerro Óbu, on trail, 100–300 m, 9°23′N, 78°48′W, *de Nevers et al. 8019* (MO, PMA); Río Diablo, 40 m, 9°23′N, 78°34′W, *Herrera et al. 1714* (MEXU, MO, PMA, STRI, US). **Veraguas**: Santa Fe region, slopes of Cerro Tute, NW of Santa Fe, 1250–1350 m, *Croat 48971* (F, MO, W); Santa Fe–Río San Luis, 8 mi. N of school, 450 m, 8°33′N, 81°08′W, *Croat 66959* (CM, ENCB, MBM, MO, PMA, QCA); Alto Piedra–Calovébora, Río Dos Bocas Valley, 350–400 m, *Croat 27367* (F, MO, PMA, US).

COLOMBIA. **Chocó**: Medellín–Quibdó, 78 km W of Bolívar, 466 m, *Croat 49286* (MO); Km 175–176, 117–118 km E of Quibdó, 465 m, 5°44′N, 76°28′W, *Croat 57485* (CHOCO, COL, JAUM, K, MO, US); Quibdó–Istmina, Km 14, <100 m, 5°32′N, 67°37′W, *Croat & Cogollo 52215* (MO); S of Río Rancherita, Km 31–32, <50 m, 5°27′N, 76°39′W, *Croat 57372* (CHOCO, COL, JAUM, MO); Quibdó–Lloro, vic. Río Atrato, ca. 150 m, 5°29′N, 76°35′W, *Croat 55979* (COL, JAUM, MO, NY); Río Capá–Río Mumbú, upriver from Lloro, 80–120 m, 5°37′N, 76°25′W, *Juncosa 1457* (MO); Quibdó–Yuto, 12 km S of

Quibdó, 60 m, 5°38′N, 76°40′W, *Croat 56261A* (CM, MO); Serranía de Baudó, Las Animas–Pato (Río Pato), 4 km S of Pato, 150 m, 5°30′N, 76°46′W, *Croat 56151* (MO); Jequedó, 41 km W of Las Animas, ca. 10 km E of Río Pato, 220 m, *Gentry & Rentería 24112* (MO). **Nariño**: Mpio. Barbacoas, Reserva Natural Río Ñambí, 1325 m, 1°18′N, 78°08′W, *Betancur et al. 4778* (MO). **Valle**: Bajo Calima region, Buenaventura–Río Calima, 6.5 km beyond Portón Tomar, 50 m, 4°02′N, 77°07′W, *Croat 61278* (AAU, B, CAS, CM, COL, CR, F, K, L, MO, NY, QCA, US); *61380* (CM, MO); road to Málaga, 6 km S of main road, 50–80 m, 3°56′N, 77°07′30″W, *Croat 69417* (AAU, COL, CR, GB, MEXU, MO, NY, QCA); 100 m, 3°55′N, 77°W, *Monsalve 892* (MO); Buenaventura–Málaga, Km 65–66, 40–65 m, 4°10′N, 77°12′W, *Croat 71055* (MO); at Km 17.5, 3°57′N, 77°01′W, *Croat & Bay 75630* (MO); Km 28, W of Buenaventura–Málaga road, 3°59′N, 77°03′W, *Bay 269* (MO); Km 35.2, 100 m, 4°N, 77°03′W, *Croat & Bay 75759* (MO); Km 44, <100 m, 4°03′N, 77°08′W, *Croat & Watt 70199* (COL, MO, NY, US); Km 52.4, 140 m, 4°03′N, 77°05′W, *Croat & Bay 75724* (MO); *75728* (MO); 11 km NW of Cali–Buenaventura Highway, 3°56′30″N, 77°01′W, *Croat 69321* (CM, MO). ECUADOR. **Carchi**: Chical, 1200–1250 m, 0°56′N, 78°11′W, *Thompson & Rawlins 761* (CM, MO).

Philodendron schottianum H. Wendl. ex Schott, Oesterr. Bot. Z. 15: 72. 1865. TYPE: Costa Rica. *Wendland s.n.* (holotype, W? lost). Schott ic. 2735–36 (neotype, here designated, W). Figures 2, 17, 365–371.

Usually epiphytic or hemiepiphytic; stem appressed-climbing, grayish green, sap strongly thyme-scented; internodes short, thick, semiglossy, 4–7.5 cm diam., broader than long, pale green to gray, epidermis thin, yellow, fragmented, without fissures; roots moderately few per node, drying dark brown to ca. 5 mm diam., epidermis semiglossy, flaking; cataphylls 16–46 cm long, sharply 2-ribbed (ribs to 1.5 cm high), usually tinged red, drying brownish yellow, often glossy (as if surface is shellacked), broadly concave to broadly D-shaped adaxially, persisting semi-intact, finally as a dense mass of whitish fibers; margins acute; **petioles** 35–83 cm long, 1–2.2 cm diam., subterete to D-shaped, firm to moderately spongy, medium green, drying yellowish brown, obtusely flattened with obtuse medial rib toward apex adaxially, surface semiglossy and obtusely striate; **blades** ovate, subcoriaceous, semiglossy, moderately bicolorous, acuminate to abruptly acuminate at apex (the acumen strongly inrolled, 2–8 mm long), cordate to sagittate at base, 30–77 cm long, (17.5)23–64 cm wide (1–1.7(2.7) times longer than wide), (0.6–1.2 times longer than petiole); upper surface dark green, semiglossy to subvelvety-matte; lower surface semiglossy or rarely matte, moderately paler; anterior lobe 23–57 cm long, 24.5–64 cm wide (1.6–2.7 times longer than posterior lobes); posterior lobes 8.5–28 cm long, 10–29.6 cm wide, obtuse to broadly obtuse; sinus usually spathulate, 8–20 cm deep; midrib flat to broadly convex, paler than surface above, convex to narrowly rounded, concolorous or slightly darker than surface below; basal veins (1)6–7(8–9) per side, with 0–1(2) free to base, most of the remainder coalesced 1–5.5 cm, 2 coalesced to 11 cm; posterior rib usually naked, 1–3 cm long; primary lateral veins 3–8 per side, departing midrib at a usually 40–70° angle, quilted-sunken to sunken, paler than surface above, convex and slightly paler than surface below; tertiary veins visible and darker than surface below; minor veins conspicuous, arising from both the midrib and primary lateral veins, moderately prominulous on drying, alternating with secretory ducts perpendicular or more frequently oblique, sometimes branching; "cross-veins" weakly parted. INFLORESCENCES erect to erect-spreading, (1)2–3 per axil; peduncle 2–9 cm long, 8–14 cm diam., pinkish red, white striate, especially toward apex; **spathe** 10–17 cm long (1.9–7 times longer than peduncle), weakly constricted, oblong-ellipsoid; spathe blade light green outside, cream, pale lineate in upper one-half inside; spathe tube green, tinged red outside, 6–9 cm long, red with conspicuous resin canals inside; **spadix** tapered to somewhat ovate, weakly protruding, 8.8–14.4 cm long; pistillate portion weakly ovoid, whitish, (2)3–4.9 cm long, 2–2.4 cm diam. throughout, 1.4–1.5 cm diam. at apex, 1.4–1.9 cm diam. at middle, 1.4–1.8 cm wide at base; staminate portion 5.7–10.8 cm long; fertile staminate portion bluntly tapered at apex, 1.1–1.4 cm diam. at base, 1.2–2.3 cm diam. at middle, 1(1.7) cm diam. ca. 1 cm from apex, broadest at upper two-thirds, broader than the pistillate portion, slightly narrower than the sterile portion; sterile staminate portion broader than the pistillate portion, 1.4–2.5 cm diam.; pistils (1)3–3.9 mm long, 1.5–1.9(3.8) mm diam., margins broadly rounded and slightly raised above the apex; ovary 4–6-locular, 1.9–2.5 mm long, 1.3–1.9(3.8) mm diam., with axile placentation; locules 1.9–2.5 mm long, 0.4–0.7 mm diam.; ovule sac not present or to 1.9 mm long; ovules 10–14(18) per locule, 2-seriate, rarely contained within translucent or transparent envelope, 0.1–0.3 mm long, longer than funicle; funicle 0.1–0.3 mm long, adnate to lower part of partition, style 0.8–1.2 mm long, 1.5–1.9(3.6) mm diam., similar to style type B; style apex barely raised, button-like, broadly concave, medial apex with a whitened margin, raised and apparently like type D on drying; stigma subdiscoid, truncate, 1.4–1.6 mm diam., 0.3–0.4 mm high, covering ± entire style apex, sometimes de-

pressed shallowly and medially; the androecium truncate, oblong, prismatic, margins irregularly 4–5-sided, sometimes scalloped, 1 mm long, 1.8–2.1 mm diam. at apex; thecae ± oblong, 0.4–0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregularly 4–6-sided, prismatic, 2.5–3.5 mm long, (1.4)1.8–2.2 mm wide. INFRUCTESCENCE with pistillate spadix 5–6 cm long, 3.5 cm diam.; berries white, 1.1 cm long, 4–4.6 mm diam.; seeds 1.4 mm long, 0.5 mm diam., cream-colored.

Flowering specimens of *Philodendron schottianum* have been collected only from March and June, but post-anthesis collections have been made from March through August. Immature fruiting collections have been collected from January, May, September, and November. The immature January fruiting collection is a clear indication that the species must flower much earlier in the dry season than March (as indicated above). Perhaps it flowers throughout the dry season. In the cloud forest regions where this species occurs the dry season would not be very severe.

Philodendron schottianum ranges from Costa Rica to Panama at (490)730 to 2250 m in *Premontane rain forest* and *Tropical Lower Montane wet forest* life zones. In Panama, this species ranges no further east than Veraguas (Cerro Tute), except for a disjunct occurrence on Cerro Jefe in Panamá Province. All Costa Rican collections are from the northern slopes of the Cordillera Central in Alajuela, Heredia, and San José, and the northern end of the Cordillera de Talamanca in the Tapantí region of Cartago Province. It is to be expected throughout much of the Cordillera de Talamanca.

Philodendron schottianum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa.* This species is distinguished by its short, thick internodes; sharply 2-ribbed cataphylls persisting as a dense mass of fibers (frequently with patches of glossy, yellowish to orange-brown epidermis); obtusely to sharply D-shaped petioles drying somewhat grayish or rarely yellowish and glossy; large, broadly ovate blades with a deep, usually spathulate sinus, usually pale-drying primary lateral veins; and rather conspicuous secretory canals between the veins; 2–3 short-pedunculate inflorescences per axil; and scarcely constricted, externally green spathes red on the tube within.

In Costa Rica and at higher elevations in Panama, such as on Cerro Colorado and on Cerro Pate de Macho (1000 to 2200 m), the petioles are subterete or obtusely flattened adaxially. At lower elevations in Bocas del Toro, Veraguas, and Coclé, the petioles become D-shaped to sharply D-shaped with erect margins, and at the lowest elevations they are nearly always wing-margined.

In Bocas del Toro Province, Panama, at middle elevations and in mesic situations, this species is most easily confused with *P. findens,* which also has sharply D-shaped petioles. *Philodendron findens* also has spathes which, like those of *P. schottianum,* are barely constricted midway. In rare situations where the blades of *P. findens* do not promptly tear into narrow segments, *P. findens* can be distinguished from *P. schottianum* by having primary lateral veins of the lower surface drying darker than the surface.

In central Panama, *P. schottianum* can also be confused with *P. llanense.* Both *P. schottianum* and *P. llanense* occur in the Cerro Jefe region, though *P. schottianum* has been collected there only once, northeast of Altos de Pacora. This collection (*Croat 68691*) exhibits most of the diagnostic features of *P. schottianum,* especially the persistent yellowish, semi-intact cataphylls, and the acutely D-shaped petioles with an obtuse medial rib (unknown in *P. llanense*), but has a blade shape midway between that of *P. schottianum* and *P. llanense* (blade length/width ratio 1.5 vs. an average of 1.4 for *P. llanense* and 1.65 for *P. schottianum*). *Philodendron llanense* differs in having at most obtusely flattened petioles and in lacking the conspicuous yellowish cataphylls of *P. schottianum. Philodendron llanense* also rarely occurs above 500 m (to 950 m), whereas *P. schottianum* only rarely occurs to as low as 500 m.

Philodendron schottianum can be confused with *P. thalassicum* and *P. alticola,* especially in Costa Rica. *Philodendron thalassicum* differs in having bluish green leaf blades that are glaucous beneath and sharply D-shaped petioles drying somewhat blackened rather than merely obtusely flattened and light yellow-brown, as in *P. schottianum. Philodendron alticola* differs in usually having narrower leaf blades (usually more than 1.8 times longer than wide) and stigma tubes exserted as minute funnels on the dried stigma.

Philodendron dodsonii may also be confused with *P. schottianum.* The former differs in occurring usually at lower elevations principally in tropical wet forest and premontane wet forest, and in having larger leaf blades, more long-pedunculate inflorescences, and longer spathes with a normal constriction above the spathe tube.

One collection, *Grayum 7333,* differs from more typical collections in having blades reportedly matte on both surfaces and lacking prominulous minor veins and conspicuous secretory ducts (so evident in other material of this species where they

alternate with the minor veins). In addition, this specimen has darker-drying petioles and more fragmentary old cataphylls as well as intact cataphylls (perhaps juvenile?) drying brown (rather than the typical brownish yellow) and a spathe with a narrowly acuminate portion extending a full 5 cm beyond the end of the spadix. On other specimens, the spadix ends only about 1 cm or less short of the end of the spathe.

Hammel et al. 14705 is unusual in lacking cataphylls, suggesting that they might have been deciduous (or forcibly removed during preparation).

Additional specimens examined. COSTA RICA. **Alajuela**: 3.5–4 mi. W of center of San Ramón, ca. 800 m, *Croat 46813* (MO); Atlantic side of Alto Palomo, 1900 m, *Lent 1845* (CR, F); Río Gorrión–Río Toro, 1700 m, 10°12′N, 84°19′W, *2996* (CR, F); Río Cariblanco Canyon, Río Cariblanco–Quebrada Quicuyal, SW of Cariblanco, 840–950 m, 10°16′N, 84°12′W, *Grayum et al. 6186* (CR, MO, NY); Río Sarapiquí, road to Colonia Virgen del Socorro, 830 m, 10°16′N, 84°11′W, *Croat 68341* (CR, MO). **Cartago**: 31 km from San José, SE of CR-2, 1750 m, *Harmon & Fuentes 6081* (UMO); Tapantí Watershed Preserve, ca. 20 mi. SW of Paraíso, 1500–1800 m, 9°43′N, 83°47′W, *Croat 47047* (MO); 1500–1800 m, *Croat & Grayum 68293* (B, K, MO); 1500–1700 m, Croat *36110* (MO); 1250–1350 m, *79018* (CR, INB, MO); *Grayum & French 5820* (MO); *Nilsson et al. 383* (CR); along Camino Raiz de Hule, SE of Platanillo, 1200–1400 m, *Croat 36824* (MO). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35778* (MO); 4 mi. N of V. Bara Blanca, 1350 m, *Croat 35620* (F, MO, PMA); Río La Paz Grande, 7.5 km N of Vara Blanca, 1270–1350 m, *Croat 36017* (MO); Río Santo Domingo, ca. 3 km E of San Rafael de Vara Blanca, Volcán Barva, 2060–2100 m, 10°11′N, 84°07′W, *Grayum 7333* (CR, MO, US); Volcán Barva, Finca Montreal, Río Volcán–Río San Fernando, 1740 m, 10°12′39″N, 84°06′45″W, *Boyle et al. 1155* (MO, NY); Volcán Barva, along Río Vueltas, 1900 m, 10°06′N, 84°04′W, *Burger & Gentry 9042* (F, US); Parque Nacional Braulio Carrillo, 1000 m, 10°16′38″N, 84°04′57″W, *Boyle 964* (CM, MO, TEX); *1223* (CR, MO); 1990 m, 10°11′03″N, 84°06′27″W, *1058* (CR, MO); 1750 m, 10°03′40″N, 84°01′W, *2432* (CR, MO, NY). **Puntarenas**: Monteverde Reserve, 1500 m, ca. 10°17′N, 84°48′W, *Croat 61194* (CM, MO, PMA); Coto Brus, Cordillera de Talamanca, 730 m, 9°01′30″N, 82°57′40″W, *Mora 14* (INB). **San José**: 4 km N of Cascajal, 7 km N of Las Nubes on CR 216, 1500–1600 m, *Utley & Utley 5259* (DUKE); Cerro de la Muerte, ca. 2000 m, *Croat 32859* (MO); Braulio Carrillo National Park, 1000–1500 m, 10°05′N, 83°57′W, *Croat 61226* (MO). PANAMA. **Bocas del Toro**: Cerro Colorado, 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69066* (CM, CR, MO, PMA); Fortuna Dam area, Chiriquí Grande–Fortuna, 1.2 mi N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60447* (CR, MO, NY, PMA, TEX); 0.3 km N of Divide, 970 m, 8°43′N, 82°17′W, *Croat & Zhu 76518* (CR, DUKE, MO, WIS). **Chiriquí**: Cerro Colorado, above San Félix, 18–27 mi. off Pan-American Highway, 1200–1500 m, *Croat 33153* (MO); 20 mi. N of Río San Félix, 2000 m, *Croat 48460* (MO, TEX); 18.5 mi. N of Río San Félix, 1660 m, 8°30′N, 81°46′W, *Croat 74991* (AAU, CAS, CM, COL, CR, G, K, MEXU, MO, QCA, US); Cerro Hornito, above Los Planes de Hornito, 1750–1900 m, 8°41′N, 82°10′W, *Croat 67979* (F, MEXU, MO, PMA); Cerro Pate Macho, NE of Boquete, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66395* (F, MO); 1800–2200 m, *48560* (MO); 1900–2000 m, *66505* (B, CM, COL, CR, DUKE, F, L, MEXU, MO, QCA, TEX, US, VDB, VEN); ca. 2200 m, *Croat 48545* (MO); 1650–2000 m, 8°50′N, 82°25′W, *McPherson 11315* (MO, PMA); Cerro Punta, above town, 2250 m, *Croat 48601* (MO); Fortuna Dam area, Gualaca–Chiriquí Grande, Río Chiriquí, 9.1 mi. beyond Los Planes de Hornito, 1300 m, *Croat 48758* (MO); Quebrada Arena, 1050 m, 8°45′N, 82°16′W, *Hammel et al. 14705* (MO). **Coclé**: El Valle region, La Mesa, N of El Valle de Antón, E edge of Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67234* (MO, PMA); 900–930 m, *37433* (F, MO); El Copé area, on western slope, just S of the old saw-works area, 700 m, 8°38′N, 80°35′W, *Croat & Zhu 76795* (MO). **Panamá**: Cerro Jefe region, 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-American Highway, 700–750 m, 9°15′N, 79°25′W, *Croat 68691* (AAU, CAS, K, MO, NY). **Veraguas**: Santa Fe region, Santa Fe–Calovébora, beyond Escuela Agrícola Alto Piedra, beyond Río Tercero Brazo, 600 m, 8°31′N, 81°08′W, *Croat 66930* (CM, MEXU, MO, NY, PMA); Río Primero Brazo, 490 m, 8°33′N, 81°08′W, *66879* (CM, CR, HUA, IBE, JBGP, MO, PMA, QCA, US); ca. 3 mi. N of the school, ca. 700 m, *Croat 49002* (MO); 1.7 mi. past the school, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76832* (MO); slopes of Cerro Tute, near Escuela Agrícola Alto Piedra, 800–1030 m, *Croat & Zhu 76872* (CAS, MO); 1050–1150 m, *Croat 48896* (CM, MO); 0.6 mi. beyond school, 730 m, *Croat & Folsom 33954* (F, MO, PMA); *34041* (MO); Cerro Tute, 1250–1350 m, *Croat 48958* (CAS, MO); 800–950 m, 8°33′N, 81°08′W, *Croat 67002* (CAS, CR, L, MO, NY, PMA).

Philodendron smithii Engl., Bot. Jahrb. Syst. 26: 540. 1899. TYPE: Guatemala. Izabal: Río Dulce at Livingston, sea level, 5°49′N, 88°45′W, *J. D. Smith 1535* (lectotype, here designated, US; isolectotype, K). Figures 364, 372, 373, 377, 378.

Usually hemiepiphytic, sometimes terrestrial or epilithic; stem usually appressed-climbing, leaf scars conspicuous, 7–15 mm long, 7–16 mm wide; internodes glossy, (1)2.2–3 cm long, 2–3 cm diam., usually longer than broad or about as long as broad, tan or gray-green to dark green, epidermis drying yellow-brown with loose flakes, fissured conspicuously; cataphylls soft, spongy, 12–20 cm long, bluntly to sharply 2-ribbed, green, dark green short-lineate, rounded at apex, drying tannish to yellowish, deciduous, intact; **petioles** 21.5–63 cm long, 4–16 mm diam., subterete, spongy, medium green, obtusely flattened with obtuse angle toward apex adaxially, surface dark short-lineate, dark with a dark purple-black ring around apex; **blades** narrowly ovate, subcoriaceous, glossy, moderately bicolorous, acuminate to long-acuminate at apex (the acumen inrolled, 1–4 mm long), cordate at base, 26.5–53 cm long, 11–31 cm wide (1.2–2.2 times

longer than wide), (0.7–1.4 times longer than petiole), margins hyaline, convex is lower half of blade, upper surface dark green, drying dark gray-green to yellow-brown, lower surface light greenish, usually drying yellow-green to yellow-brown, sometimes olive-green; anterior lobe 18–41 cm long, 18–30 cm wide, (1.8–2.9 times longer than posterior lobes); posterior lobes (3.2)7.5–16 cm long, 8.7–14.2 cm wide, obtuse to broadly rounded; midrib flat to broadly convex, paler than surface above, prominently raised, concolorous below; basal veins (3)4–5(6) per side, with 0–1 free to base, 1–2 coalesced (1.8)2.5–5.5(7.5) cm; posterior rib not at all naked or briefly so, usually 1–1.5 cm (rarely to 2 cm); primary lateral veins 3–6 per side, darker than surface below, departing midrib at a 50–70° angle, ± straight, eventually weakly arcuate to the margins, sunken above, convex below; interprimary veins weakly raised, darker than surface below; minor veins numerous, sparsely visible, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 2 per axil; peduncle 9–22 cm long, (1)9–12 mm diam., medium green, moderately spongy; **spathe** ± erect, 8.8–19.8 cm long, (0.5–1.4 times longer than peduncle), prominently constricted at anthesis; spathe blade yellowish green to green, glossy outside, 7 cm long, 1.7 cm diam., whitish green, minutely white-dotted, sometimes orange-striate inside; spathe tube ellipsoid, green outside, 8.5 cm long, 2.5 cm diam., light red to maroon (B & K red-purple 2/10) inside; **spadix** stipitate 6–15 mm long; gradually to bluntly tapered to apex, 9.3–16.9 cm long; pistillate portion pale green to greenish yellow, 3.3–5.2 cm long in front, 2.2–2.5 cm long in back, 1.4 cm diam. at apex, 1.3–1.6 cm diam. at middle, 1.6 cm wide at base; staminate portion 6.5–11.3 cm long; fertile staminate portion creamy white, 9–12 mm diam. at base, 1–1.2 cm diam. at middle, 5–7 mm diam. ca. 1 cm from apex, broadest at the middle, narrower than the pistillate and sterile portions; sterile staminate portion broader than the pistillate portion, creamy white, (9)1.1–1.5 cm diam.; pistils 1.8–2.3 mm long, 1.1 mm diam., creamy white; ovary 6–8-locular, 0.9–1.2 mm long, 1 mm diam., usually with basal, somtimes sub-basal placentation; locules 0.9–1.1 mm long, 0.3–0.4 mm diam.; ovule sac 0.9(1.2) mm long; ovules 1 per locule, contained within transparent ovule sac, 0.3–0.4 mm long, about as long as funicle; funicle 0.3–0.4 mm long (can be pulled free to base), style 0.6–0.8 mm long, 1.1 mm diam., similar to style type B; style apex ± sloping; stigma subdiscoid, greenish yellow, 1 mm diam., 0.3 mm high, covering entire style apex; the androecium irregularly 5–6-sided, sometimes oblong or quadrangular, 1.6–1.9 mm long, 0.9–1.2 mm diam. at apex; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another and nearly contiguous; sterile staminate flowers blunt, irregularly 4–6-sided, sometimes prismatic, (1)1.6–2 mm long, (1.2)1.7–1.8 mm wide. Berries white or sometimes yellowish; seeds 1 per locule, tan, oblong, 2 mm long, 0.8 mm diam.

Flowering in *Philodendron smithii* occurs principally in the dry season, and flowers have been collected from December to April (but also July). Post-anthesis collections are common from February through July but with a few in October, November, and December. The latter, especially those in October and November, are the most aberrant, since even if this species is cued to flower by the onset of the dry season (which appears to be the case), they would appear to have flowered too early. This may be explained by the fact that the dry season starts much earlier in Mexico and Guatemala than in Costa Rica and Panama.

Philodendron smithii ranges from Mexico (mostly in Chiapas, Tabasco, and Quintana Roo) to Guatemala, Honduras, and Nicaragua on the Atlantic slope at 40 to 1630 (mostly less than 600) m elevation. It is known from "Selva Alta Perennifolia" and "Selva Mediana Subperennifolia" in Mexico as well as from *Tropical moist forest* and *Subtropical wet forest* in Guatemala.

Philodendron smithii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by its conspicuously fissured tan internodes, which are about as long as to longer than broad; sharply two-ribbed, deciduous cataphylls; spongy subterete petioles; usually blackish, narrowly ovate-cordate leaf blades; long-pedunculate inflorescences; and externally green spathes that are maroon inside the tube.

Philodendron smithii is not easily confused with any other species in Central America. It is most similar to *P. panamense,* which is endemic to Panama, and shares with that species similarly dark-drying ovate-triangular, long-petiolate blades and long-pedunculate inflorescences. *Philodendron panamense* differs in having much shorter internodes (shorter than broad on flowering plants), weakly one-ribbed cataphylls, moderately firm petioles, and spathes green on the tube outside with a white blade and greenish white throughout within (vs. green throughout outside and maroon on the tube within for *P. smithii*).

Philodendron smithii is also similar to *P. straminicaule* and *P. wilburii,* both from Costa Rica and

Panama and both differing in having stems drying gray-green to grayish or stramineous rather than conspicuously yellow-brown as in *P. smithii.*

Mayo (1986) reported that *P. smithii* lacks superficial resin canals in the spathe and that instead resin production has entirely shifted to the spadix. However, we observed resin canals on the inner surface of both the spathe and the blade in this species.

A noteworthy collection is *Standley 52776* from the Lancetilla Valley in Honduras. It has leaf blades with broadly flaring lobes, but otherwise does not differ from other collections.

One outlying collection in Mexico, from the state of Querétaro at 450 m (*López 539*), is believed also to be this species.

Mayo (1989) reported style type E for *Croat 47913,* but my investigations of flowers of that collection showed no evidence of an annulus on the ovary, and while there was a slight depression in the style apex, the latter was not deemed sufficiently funnel-shaped to qualify for anything except a type B style.

The type specimens (*J. D. Smith 1535*), though unequivocal, were distributed by Engler with a printed label bearing the name *Philodendron donnell-smithii,* but no such name appears in Engler's publications.

Additional specimens examined. BELIZE. Camp 1, flood plain of the Caves Branch River, *Whitefoord 1263* (BM); Sibun River, Gracie Rock, *Gentle 1715* (MICH). **Cayo**: near Camp 6, *Gentle 2424* (CM, MICH). **Stann Creek:** Stann Creek Valley, 250–300 ft., *Schipp S-304* (F, GH, MO); Leoniel Valley, *Gentle 3513* (MICH, NY); Cockscomb Mountains, 2 km N of Victoria Peak, 300–500 ft., *Gentry 8033* (MO). **Toledo**: Richardson Creek, affluent of Bladen Branch, Maya Mountains, 100–250 m, 16°33′N, 88°47′W, *Davidse & Brant 31877* (BM, GH, MO); 80–420 m, 16°32–33′N, 88°45–46′W, *32052* (MO); Richardson Creek–Quebrada de Oro, canyon along Bladen Branch, 100–200 m, 16°31–33′N, 88°46–49′W, *Davidse & Brant 32230* (MO); Columbia Forest Station, 1.5 mi. from Maya village of San José, *Gentry 8132* (MO); *Croat 24360* (MO); *Dwyer 9891* (MO); Southern Mayo Mountains, Bladen Nature Reserve, 400–500 m, 16°30′22″N, 88°54′54″W, *Davidse & Meadows 35827* (BRH, CM, MO, SEL); Big Fall Estate, ca. 3 airline km NE of village of Big Fall, 40 m, 16°16′22″N, 88°52′27″W, *Davidse 35628* (BRH, MO). GUATEMALA. **Alta Verapaz**: Tucurú–El Estor, 9 mi. up road to Oxec, 700 m, *Croat 41652* (MO); 800 m, *41694* (MO); 4 mi. up road to Oxec, 500 m, *41611* (MO); road to El Estor, 5 mi. W of Tucurú, 12 mi. E of Hwy. CA-14 to Cobán, 600 m, *Croat 41512* (MO); Pantín, below Tamahú, ca. 600 m, *Standley 70512* (F); *70513* (F); along Quiché Highway, ca. 12 km W of San Cristóbal, ca. 1100 m, *Standley 89738* (F); near Tactic, ca. 1500 m, *Standley 92022* (F); vic. of Cobán, ca. 1300 m, *Standley 92676* (F); ca. 20 km W of Cobán at Cruz Max, 1500 m, *Castillo & Hodel 1100* (MO); vic. of Cubilgüitz, 1.5–2 mi. S, 300–350 m, *Steyermark 44404* (F, MO); Río Carchá, Cobán–San Pedro Carchá, ca. 1360 m, *Standley 90086* (F); Río Polochic, below Tamahú, ca. 975 m, *Standley 91990* (F). **Baja Verapaz**: Biotopo del Quetzal, 1630 m, *Martínez et al. 23011* (MEXU). **Izabal**: Quiriguá vicinity, 75–225 m, *Standley 23911* (US); ca. 4 mi. SW of Puerto Barrios, 50 m, *Croat 41823* (MO); ca. 7 mi. S of Puerto Barrios, 50 m, *Croat 41804* (MO); Lago Izabal vicinity, 0–600 m, 89°0–25′W, 15°15–35′N, *Jones et al. 3046* (F, NY); near Entre Ríos, ca. 18 m, *Standley 72746* (F); Bananera–La Presa, Montaña del Mico, 40–300 m, *Steyermark 38184* (F); Montaña del Mico, between Milla 49.5 and ridge 6 mi. from Izabal, 65–600 m, *Steyermark 38509* (F); *38613* (F). **Petén**: La Libertad, *Lundell 2994* (MICH, US); Uaxactun, *Bartlett 12426* (MICH, UC, US); El Paso, *Lundell 1572* (CM, MICH); *2929* (MICH); Santa Teresa, *Lundell 2888* (GH, MICH); Tikal National Park, 2 mi. S of entrance, 500 ft., *Croat 24700* (MO); Finca Yalpemech, Río San Diego, 50–150 m, *Steyermark 45315* (CM, F, NY, US). **Zacapa**: 41 mi. S of turnoff to Petén Morales, 150 m, *Croat 41874* (MO). HONDURAS. Potrero, along Highland Creek, *Wilson 484* (NY). **Atlántida**: San Alejo vicinity, near Río San Alejo, 150–270 m, *Standley 7699* (F); San José de Texíguat, SE of Tela, *Nelson 10732* (TEFH); Lancetilla Reserve, ca. 2 mi. WSW of Tela and S of main hwy., 70–90 m, 15°44′N, 87°27′W, *Croat & Hannon 64588* (CM, F, K, MO, US); 100 m, *Molina & Molina 25650* (EAP, F, NY); 20–600 m, *Standley 52776* (F, US); 20–600 m, *Standley 52980* (F, US); 45 m, *Allen 6143* (EAP, F); 10–150 m, *Croat 42656* (MO), *42675* (MO); 19.2 km E of Tela on Tela–Ceiba Highway, near San Francisco de Soco, 50–100 m, 15°44′N, 87°21′W, *Brant & Zúñiga 2845* (EAP, MO, US); Campamento Quebrada Grande, ca. 10 km SW of La Ceiba, 80–180 m, 15°42′N, 86°51′W, *Liesner 26179A* (MO). **Cortés**: Lago de Yojoa, 650 m, *Croat 42761* (MO); Agua Azul, *Allen 6448* (EAP, F). **Lempira**: Montaña de Celaque, between Gracias and top of Cerro Celaque, 14°33′N, 88°39′W, *Davidse & Zúñiga 34540* (MO). **Olancho**: Río Wampusito, Dulce Nombre de Cuimí, 500–700 m, 15°15′N, 85°25′W, *Nelson & Clewell 439* (EAP, FSU, MO); San Esteban–Bonito Oriental, Río Grande, 3.3 mi. SW of border with Colón Dept., 350–400 m, 15°31′N, 85°42′W, *Croat 64524* (AAU, CAS, EAP, GB, K, MEXU, MO, NY, P). MEXICO. **Chiapas**: Mpio. La Trinitaria, Lagos de Montebello National Park, at Cinco Lagunas, 1600 m, *Breedlove 68620* (CAS); 10 km ENE of Dos Lagos, above Santa Elena, 1170 m, *Breedlove & Almeda 57585* (MO); 1000 m, *Breedlove 56538* (CAS); Mpio. Las Margaritas, confluence of Río Ixcán and Río Lacantum, 300 m, *Breedlove & McClintock 34198* (MO); 12 km E of Tziscao, 1200–1300 m, *Davidse et al. 29886* (MO); Palenque–Boca Lacantum, Mpio. Ocosingo, Nuevo Guerrero, 340 m, *Martínez 18108* (MO); Ojo de Agua de San Javier, a 23 km al SE de Nuevo Guerrero, road to Boca Lacantum, 370 m, *Martínez 16929* (MO); 2 km N of Naja, trail to Chancala, 900 m, *Martínez 21320* (MEXU), *21328* (MEXU), *21331* (MEXU); San Cristóbal–Palenque, San Cristóbal de las Casas, 97 km NE of San Cristóbal, 1130 m, 17°27′N, 92°04′W, *Hammel et al. 15625* (K, MEXU); 70 km SW of Palenque, *Breedlove 47180* (CAS, MO); Laguna Ocotalito, 12 km N of Monte Líbano, trail to Chancala, 950 m, *Martínez 17605* (MO); near lake at Naja, 300 m, *Breedlove 49951* (CAS); Mpio. Pueblo Nuevo Solistahucán, 3 km NW of town, 6700 ft., 17°30′N, 92°40′W, *Will 412* (CAS, DH); San Fernando–Maravillas, 840–940 m, 16°53′N, 93°16′W, *Croat & Hannon 65003* (COL, F, K, MEXU, MO, NY, US); 20–30 mi. SW of El Jocote, road to Motozintla de Mendoza, 700–900 m, *Croat 40707* (B,

MEXU, MO); 1 mi. N of Escuintla, 100 m, *Croat 43802* (MO); 200 m, *Croat 40134* (MO); 160 m, *40295* (B, K, MEXU, MO); 210 m, *Croat 40317* (MO); 1000 m, *Croat 40588* (MO); 700 m, *Croat 40660* (B, MEXU, MO); 550 m, *Breedlove 56538* (CAS); ca. 400 m, *Croat 40190* (MO, NY); 460 m, *40271* (MO); 350–370 m, *40223* (MO); 0.6 mi. N of Tapulula, 35.6 mi. SSE of Pichucalco, 750 m, 17°16′N, 93°01′W, *Croat & Hannon 65285* (B, MO); 8 mi. N of Pichucalco, 80 m, *Croat 40079* (CM, L, MEXU, MO, PMA, US). **Oaxaca**: Uxpanapas region near Sarabia, 52 km E of main highway, 100 m, 17°10′N, 94°32′W, *Hammel & Merello 15579* (MEXU, MO); Chiltepec, 30 m, *Sousa 1732* (MEXU). **Queretaro**: Mpio. Jalpan, Río Las Paguas, S of Tanchanaquito, 450 m, *López 539* (MO). **Quintana Roo**: 110 km SW of Chetumal, 100 m, *Davidse et al. 20172* (MEXU, MO). **Tabasco**: 3.1 mi. E of Teapa, 150 m, 17°33′N, 92°59′W, *Croat & Hannon 65364* (MO); ca. 9 km E of Teapa, cultivated, *Mayo 85* (K, MO); base of Cerro de Madrugal, ca. km 4 SE of Teapa, 40 m, *Croat 40133* (MO); ca. 300 m, *47913* (CM, G, MEXU, MO, US); Mpio. Macuspana, Centro Recreativo de Agua Blanca, 7 km from the Villahermosa–Escarcega Highway, *Cowan & Zamudio 3351* (CAS, MEXU, MO, NY); Mpio. Tacotalpa, 0.2 km NW of Tapijulapa, *Cowan et al. 3530* (CSAT). NICARAGUA. **Jinotega**: Jinotega–Matagalpa, ca. 5–8 mi. SW of Jinotega, 1500 m, *Croat 43059* (MO). **Río San Juan**: Río Santa Cruz–Caño Santa Crucita, La Palma, 40–60 m, 11°2–4′N, 84°24–26′W, *Stevens 23432* (MO). **Zelaya**: Caño Monte Cristo, vic. Campamento Germán Pomares, ca. 10 m, 13°35′N, 83°51′W, *Moreno 14841* (MO); Cerro La Calera, 4 km N of Siuna, 350 m, *Neill 4290* (BM, MO); Cerro Waylawás, ca. 100–268 m, 13°39′N, 84°48–49′W, *Stevens 7380* (MO); ca. 80 m, ca. 13°39′N, 84°49′W, *Pipoly 4406* (MO).

Philodendron sousae Croat, sp. nov. TYPE: Mexico. Chiapas: Mpio. Ocosingo, Río Santo Domingo at Santo Domingo, 490 m, *Davidse et al. 20450* (holotype, MO–2946607; isotype, MEXU). Figures 379, 380.

Planta hemiepiphytica; internodia usque 3.5 cm longa, 8–15 mm diam.; cataphylla incostata, decidua; petiolus semiteres, 29–54 cm longus, 8–12 mm diam.; lamina ovato-cordata, 28–55 cm longa, 12.5–28 cm lata, in sicco brunnea vel olivacea supra, virella vel flavibrunnea infra; nervis lateralibus 1 3–4; inflorescentia usque 4; spatha 15–21 cm longa, lamina spathae extus cremea, tubo spathae albo, in superficiebus ambabus saturate suffuso rubro aut purpureo; pistilla 6–8-locularia; loculi 2-ovulati.

Hemiepiphytic; stem probably scandent; internodes to 3.5 cm long, 8–15 mm diam., yellow-brown to dark brown, epidermis drying smooth to wrinkled, sometimes fissured closely; roots drying reddish brown, thin, elongate, drying 3–4 mm diam., few per node; cataphylls 14 cm long, unribbed, deciduous; **petioles** 29–54 cm long, 8–12 mm diam., ± terete, drying yellow-brown; sheathing 3–6.5 cm; **blades** ovate-cordate, subcoriaceous, gradually acuminate at apex, conspicuously cordate at base, 28–55 cm long, 12.5–28 cm wide (2.2 times longer than wide), (about as long as petiole), drying subcoriaceous, upper surface drying brown to olive-green, lower surface drying greenish to yellowish brown, smooth or minutely ridged; anterior lobe 23–36 cm long, 21–27 cm wide (2.8–3 times longer than posterior lobes); posterior lobes 8–12 cm long, 10–13 cm wide; sinus parabolic; midrib drying broadly convex and usually paler than surface above, drying narrowly convex and usually concolorous below; basal veins 3–5 per side, free to base, several coalesced to 1–2 cm, occasionally 2 fused to 3.5 cm; posterior rib usually not at all naked, sometimes obscurely so for about 1 cm; primary lateral veins 3–4 per side, departing midrib at a 60–70° angle, weakly arcuate to the margins, drying weakly raised and usually paler than surface above, drying raised below; minor veins arising from both the midrib and primary lateral veins. INFLORESCENCES to 4 per axil; peduncle 6.5–13 cm long, ca. 1 cm diam.; **spathe** 15–21 cm long (1.6–2.3 times longer than peduncle), with resin canals on inner surface, visibly constricted above the tube; spathe blade cream outside; spathe tube white, heavily tinged red or purple on both surfaces, spathe tube 5–11 cm long; **spadix** sessile; 6–14 cm long; pistillate portion cylindrical-tapered toward the apex, 2.4–4.1 cm long, 4–9 mm diam. at apex, 5–10 mm diam. at middle, 6–10 mm wide at base; staminate portion 3.6–10 cm long; fertile staminate portion (4)9 mm diam. at base, 6–12 mm diam. at middle, 3–7 mm diam. ca. 1 cm from apex, broadest at or below middle, broader than the pistillate portion; sterile staminate portion not obvious; pistils 0.5–2.7 mm long, (0.7)1.8–2.7 mm diam.; ovary 6–8-locular, 0.4–1.4 mm long, 0.7–2.7 mm diam., with basal (to sub-basal) placentation; locules 0.4–1.4 mm long, 0.9 mm diam.; ovule sac 0.3 mm long; ovules 2 per locule, contained within a translucent, gelatinous ovule sac, 0.1–0.2 mm long, much shorter than funicle; funicle 0.7–0.9 mm long, style 0.4 mm long, 0.4–1.5 mm diam., similar to style type D; stylar canals emerging at base of apical depressions and arranged separately in a ring on orifices around center; style apex flat; style boss moderately shallow to moderately prominent; stigma discoid, 0.4 mm diam., 0.1 mm high, covering entire style apex; thecae oblong to weakly ovate, 0.2–0.4 mm wide, divaricate.

Flowering in *Philodendron sousae* occurs in the early rainy season, and specimens have been collected in May and August. Fruits are not known.

Philodendron sousae is endemic to Mexico in Chiapas, at 490 to 1400 m elevation on the Atlantic slope in regions of "Selva Alta Perennifolia."

Philodendron sousae is a member of *P.* sect. *Ca-*

lostigma subsect. *Macrobelium* ser. *Macrobelium*. This species is characterized by its ovate-cordate, light greenish-brown-drying blades with three to four primary lateral veins per side and three to five free to weakly coalesced basal veins, which are usually not at all naked. Also characteristic are the inflorescences, ranging up to four per axil and with the spathe more or less oblong and constricted somewhat above the tube. The spathe tube is white and heavily tinged with red or purple on both surfaces.

Philodendron sousae is most easily confused with some material of *P. advena* (from the Pacific slope), which dries a similar light brown to greenish brown (not dark brown typical of most material). The latter differs in having a more or less ellipsoid spathe, scarcely or not at all constricted above the tube.

Philodendron sousae may also be confused with *P. breedlovei*, which has somewhat similar blades that dry a similar color. The latter species has narrower blades, to 1.8 cm long, a single inflorescence per axil, and about 20 ovules per locule (vs. blades usually broadly ovate, averaging 1.4 times longer than wide, four inflorescences per axil, and 1–3 ovules per locule).

Philodendron sousae was first collected by D. E. Breedlove in 1972. It is named in honor of Mario Sousa (MEXU), co-editor of *Flora Mesoamericana* (Davidse et al., 1995), who (in the company of Gerrit Davidse) collected the type specimen.

Additional specimens examined. MEXICO. **Chiapas**: Mpio. Cintalapa: 4 km W of La Ciénega, 38 km W of Las Cruces, Oaxaca–Chiapas border, 1400 m, *Breedlove 25142* (DS); Mpio. Ocosingo, vic. Centro de Población Velasco Suárez (Selva Lacandona), 570 m, 16°47′N, 91°17′W, *Calzada et al. 744* (MO); Laguna Ocotal Grande, ca. 25–30 km SE of Monte Líbano (ca. 45 km E of Ocosingo), 950 m, *Dressler 1589* (GH).

Philodendron squamicaule Croat & Grayum, sp. nov. TYPE: Panama. Coclé: vic. El Copé, on western slope, just S of the old saw-works area, 700 m, 8°38′N, 80°35′W, 12 July 1994, *Croat & Zhu 76798* (holotype, MO–4613255–8; isotypes, B, CAS, CM, COL, CR, F, G, K, MEXU, NY, PMA, US, VEN). Figures 374, 381–384.

Planta hemiepiphytica; internodia brevia, 1–8 cm longa, 2–3.5 cm diam., dense squamata; cataphylla 27–34 cm longa, incostata, rosea vel rubella aut rubribrunnea, persistentia semi-intacta; petiolus teres vel subteres, 28–61 cm longus, 1 cm diam., dense squamatus, squamae purpurascentes; lamina ovato-triangularis, 26–53 cm longa, 17.5–40 cm lata, sagittato-cordata basi; nervis lateralibus 1 dense puberulis infra; inflorescentia usque 5; pedunculus 3.5–8 cm longus, olivaceus, dense squamatus; spatha 15–17 cm longa; lamina spathae extus viridalba, intus diluta viridi, suffusa rubra, dense squamata; tubo spathae omnino viridi, suffuso rubro; pistilla (3)4(5)-locularia; loculi 20–28-ovulati.

Hemiepiphytic; appressed-climbing, stem 3–20 cm long; internodes short, densely scaly with ± deltoid, sometimes bifurcated scales, mixed with fewer acicular scales, drying reddish brown, 1–8 cm long, 2–3.5 cm diam., longer than broad, semiglossy, dark green, soon gray-green, finally tannish to brownish, drying straw-colored to reddish brown to brown, completely hidden by old cataphylls; roots few per node, slender, drying brownish; cataphylls fleshy, 27–34 cm long, unribbed to bluntly 2-ribbed, yellow-green, pink to reddish, or reddish brown, densely long-scaly throughout with a sparse underlay of tuberculate structures, drying reddish brown, persisting as semi-intact pale fibers, sometimes with patches of epidermis, soon deciduous; margins folded in to form groove. LEAVES erect-spreading; **petioles** 28–61 cm long, ca. 1 cm diam., erect-spreading, terete to subterete, purplish to dark brown, surface densely scaly, 1.5–4 mm long, flattened, with a sparse underlay of tubercules; sheathing briefly only near or at the base; petiolar scales of two types, short purplish scales deltoid or broader than high, less than 0.2 mm high, these interspersed with much longer, spreading light green acicular scales, 3–5 mm long, both types of scales drying reddish brown; **blades** ovate-triangular, thinly coriaceous to subcoriaceous, conspicuously bicolorous, short acuminate to acute at apex, sagittate-cordate at base, 26–53 cm long, 17.5–40 cm wide (1–1.5 times longer than wide), (0.7–1.1 times longer than petiole), broadest at the petiole attachment, margins hyaline, upper surface medium to dark green, semiglossy to sometimes almost matte above, slightly paler, light to silvery-green, glossy to semiglossy below, drying reddish brown on both surfaces; sometimes with sparse whitish raphide cells; anterior lobe 21–28 cm long, 18–26 cm wide (2.2–2.8 times longer than posterior lobes), margins straight to weakly concave; posterior lobes 8–10.7 cm long, 7.1–11.5 cm wide, directed toward the base to somewhat outward, broadly rounded; sinus parabolic to hippocrepiform on younger leaves, mitered on older leaves, 3.5–17 cm deep; midrib flat to sunken or deeply sunken and concolorous above, convex to broadly round-raised, concolorous to paler to light reddish below; basal veins 5–12 per side, with 0(1) free to base, third and higher order veins coalesced 2–6 cm long; posterior rib naked for 3–4.5 cm, densely scaly on both upper and lower edges; primary lateral veins 5–9 per side, departing midrib at a 30–45° angle (55° angle near base), moderately straight to the margins

(the lowermost veins somewhat branched near the margins), deeply sunken and concolorous above, brown to reddish, round-raised and densely puberulent below; tertiary veins visible, slightly raised, darker than surface; minor veins moderately distinct below, arising from both the midrib and primary lateral veins; "cross-veins" sometimes moderately distinct on lower surfaces on drying. INFLORESCENCES to 5 per axil; peduncle 3.5–8 cm long, olive-green, densely scaly, especially near apex, peduncle and spathe with scales of 2 lengths, both long and acicular, 1–2 mm long, much shorter and broader deltoid to tuberculate; **spathe** 15–17 cm long, 2–4.8 times longer than peduncle, moderately constricted above the tube, green, densely to sparsely scaly outside, shortly acuminate at apex; spathe blade sometimes greenish white outside, to 5.5 cm diam., light green, tinged red near base inside; spathe tube ± ellipsoid, green, tinged red, covered with greenish scales (except for 5 mm along margin to 3 cm along infolded edge near base) outside, ca. 6 cm long, to 3.5 cm diam., reddish violet inside except greenish near tip inside; **spadix** 13.2 cm long; pistillate portion pale green to dirty-white, to 4.2 cm long in front, 3.6 cm long in back, 12 mm diam. at apex, 14 mm diam. at middle; staminate portion 11.5 cm long; fertile staminate portion 1.2 cm diam. at base, 1 cm diam. at middle, 7 mm diam. ca. 1 cm from apex; sterile staminate portion 1.2 cm diam.; pistils 1.22 mm diam.; ovary (3)4(5)-locular, with axile placentation; locules 1–1.2 mm long; ovules 20–28 per locule, 2-seriate, ca. 0.2 mm long, longer than funicle; style similar to style type D; style apex flat; style boss narrow, fairly shallow; stigma hemispheroid, 0.7–0.8 mm diam., 0.2 mm high; the androecium prismatic, margins irregularly 4–6-sided, 1.4–1.6 mm long, 1.4–1.6 mm diam.; sterile staminate flowers prismatic, margins irregularly 4–6-sided, 1.1–1.2 mm diam. INFRUCTESCENCE with peduncle to 11 cm long, 8–11 mm diam.; spathe to 23 cm long, 1.7 cm diam., dark punctate in part and drying light brown inside; spathe tube 9–9.5 cm long, reddish, spathe blade to 14 cm long; spadix to 21 cm long; pistillate spadix 6–8.5 cm long, 3.2 cm wide; pistils 4.2 mm long, 2.7 mm diam.; locules to 3.3 mm long; fertile staminate spadix 11.5 cm long, 1.1 cm diam. midway; sterile staminate spadix 2.5 cm long, 1.4 cm diam.; staminate flowers to 3.3 mm long; berries white; seeds to 18 per locule, 1 mm long. JUVENILE plants terrestrial, scandent; lower surface of blades purplish violet. PREADULT plants with internodes 2–30 cm long, 0.5–1.2 cm diam.; petioles 8.5–18.5 cm long, 2–3 mm diam.; blades 14–28 cm long, 15–22 cm wide.

Flowering in *Philodendron squamicaule* occurs in the early rainy season from May through August. Mature fruits have been collected in early December.

Philodendron squamicaule ranges from Costa Rica to Esmeraldas Province, Ecuador, from <100 to 1250 m elevation in pluvial forest, *Premontane wet forest,* and *Premontane rain forest* life zones. In Central America it has not been collected below 550 m elevation.

Philodendron squamicaule is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is recognized by its appressed-climbing habit, moderately thin, triangular-ovate, semiglossy blades, and especially by its scaly stems, cataphylls, petioles, peduncles, and outer surfaces of spathes and densely puberulent major veins on the lower blade surface.

Philodendron squamicaule is apparently closest to *P. serpens* Hook. f., which was described from a cultivated plant from an unknown Colombian locality. The latter species differs in having oblong-ovate blades, sometimes with a constriction above the posterior lobes, with 4–5 basal veins on the most well developed blades (in contrast to 6–12 basal veins). In addition, *P. squamicaule* has a coarse row of scales extending along both edges of the posterior rib and densely puberulent primary lateral veins, neither of which was described for *P. serpens. Philodendron serpens* also differs in having glabrous, rather than scaly, peduncles and spathes.

Philodendron squamicaule is probably related to *P. verrucosum,* which also has densely scaly petioles. That species differs, however, in having longer petioles (more than 30 cm long vs. less than 30 cm for *P. squamicaule*), and broadly ovate blades that are velvety and matte above and matte with frequently purplish areas along the veins below (vs. usually solid green below in *P. squamicaule*). Both species have a similar number of primary lateral veins, but the veins are much more closely spaced in *P. squamicaule* than *P. verrucosum.*

Additional specimens examined. COSTA RICA. **Heredia**: N of Quebrada Tigre, from Finca El Plástico (ca. 8 km SW of Las Horquetas), 450–550 m, 10°18′N, 84°02′W, *Grayum & Sleeper 6523* (CR, MO, US); Zona Protectora, between Río Peje and Río Gúacimo, Volcán Barba, 750 m, *Grayum & Schatz 3250* (DUKE); Sarapiquí, P. N. Braulio Carrillo, El Ceibo, 750 m, 10°17′50″N, 84°04′25″W, *Boyle et al. 2897* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 4.3 km N of the Continental Divide, 590 m, 8°46′N, 82°14′W, *Croat & Grayum 60197* (K, MO, PMA). **Coclé**: 5–5.5 mi. N of El Copé, 850 m, 8°38′N, 80°35′W, *Thompson 4731* (CM); 680–770 m, 8°39′N, 80°36′W, *Croat 74836* (MO, PMA, US); 710–800 m, *68764* (MO, NY).

Veraguas: Alto Piedra–Calovébora, 0.5 mi. N of Alto Piedra, Parque Nacional Cerro Tute, 800–1030 m, *Croat & Zhu 76906* (CR, MO, NY); ca. 5 mi. N of Alto Piedra, 670 m, 8°33′N, 81°08′W, *Croat 66962* (CM, F, MO); 1250–1350 m, *Croat 48959* (MO).

COLOMBIA. **Chocó**: between Medellín and Quibdó, 60 km W of Bolívar, 800 m, *Croat 49271* (MO); 5.5 km E of Tutunendo, 23.5 km E of Quibdó, 150 m, 5°44′N, 76°29′W, *Croat 56227* (COL, JAUM, MO); km 208.5, 9 km W of Tutunendo, ca. 9 km E of Quibdó, <100 m, 5°39′N, 76°40′W, *Croat 56204* (COL, JAUM, MO); Quibdó–Bolívar, Km 175–176, 117–118 km E of Quibdó, 5°44′N, 76°20′W, *Croat 57481* (CHOCO, COL, MO); Quibdó–Lloro, vic. Río Atrato, ca. 150 m, 5°29′N, 76°35′W, *Croat 55996* (COL, JAUM, MO, PMA). **Valle**: Buenaventura–Cali, 14 km SE of Río Sabaletas, 53 km ESE of Queremal, 270, 3°42′N, 77°51′W, *Croat & Watt 70458* (MO). ECUADOR. **Esmeraldas:** Lita–San Lorenzo road (based on *Dodson 18645*), cultivated at Río Palenque, *Croat 73857* (MO).

Philodendron squamipetiolatum Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario above El Copé, ca. 6 mi. N of El Copé, 710–800 m, 8°39′N, 80°36′W, 23 June 1994, *Croat 68767* (holotype, MO–3591312–4; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, F, G, GH, HMNM, K, M, MEXU, NY, PMA, RSA, S, SCZ, TEX, US, VEN). Figures 375, 385–388.

Planta hemiepiphytica; internodia 3–17 cm longa, 6–15 mm diam., atriviridis, squamis approximatis, scalariformibus, caespitosis, transverse orientibus; cataphylla usque 29 cm longa, incostata, squamata, persistentia nodis superioribus, mox decidua; petiolus 6–16 cm longus, usque ca. 6 mm diam., teres; lamina ovata, rotundata vel subcordata basi, 15–37.5 cm longa, 9.5–29 cm lata; inflorescentia 1–2; peduculus subteres, 6–8 cm longus, dense squamatus; spatha 11–15.5 cm longa, 2–2.5 cm diam.; lamina spathae extus viridi, dense squamata, intus atrirubello, tubo spathae extus viridi, intus atrirubello; pistilla 5–6-locularia; loculi 20–30-ovulati.

Appressed-climbing hemiepiphyte, occurring on understory trees in primary forest, fertile ca. 6 cm above the ground; stems trailing when juvenile, loosely appressed-climbing as adults; internodes 3–17 cm long, 6–15 mm diam., dark green, soon dark brown, drying yellow-brown, closely ridged-fissured with the surface moderately glossy, granular and with close, scalariform, tufted transversely oriented scales; cataphylls to 29 cm long, terete, unribbed, green and densely whitish scaly, promptly weathering to a loose semiorganized network of slender, pale fibers with fragments of epidermis, the fibers persisting at upper nodes, but soon completely deciduous; **petioles** erect to spreading, 6–16 cm long, to ca. 6 mm diam., terete, matte, dark green, surface densely covered with antrorse light green scales throughout (these ca. 6 mm long), densely granular-scurfy; **blades** somewhat pendent when young, spreading with petioles when mature, ovate, subcoriaceous, acuminate at apex, rounded to subcordate at base, 15–37.5 cm long, 9.5–29 cm wide (ca. 1.2–2.1 times longer than wide), (1.6–2.3 times longer than petiole), upper surface dark green, weakly glossy (subvelvety), drying dark brown, lower surface matte and much paler, drying yellow-brown; posterior lobes broadly rounded; sinus arcuate; midrib narrowly sunken and paler above, round-raised to thicker than broad, darker and densely puberulent below; basal veins 2–6(9) per side, with all free to base, or sometimes 3–5 pairs coalesced up to 1.5 cm, posterior rib sometimes lacking; primary lateral veins 5–7 per side, departing midrib at a 50–55° angle, weakly quilt-sunken above, round-raised to thicker than broad, darker and densely puberulent below; minor veins flat but distinct and darker than surface below, some intermittent; "cross-veins" distinct, moderately raised on drying. INFLORESCENCES 1–2 per axil; peduncle subterete, 6–8 cm long, densely scaly; **spathe** 11–15.5 cm long, 2–2.5 cm diam. when furled, to 6.5 cm wide, and constricted somewhat when flattened, green outside, especially below, densely scaly (the scales whitish), deep reddish inside, especially in the tube; **spadix** yellowish white, 9.7–13.5 cm long, to 1.3 cm diam., only weakly constricted midway; pistillate portion 2.7–4.7 cm long in the front, 0.7–1.4 cm diam.; staminate portion 7–8.8 cm long; fertile staminate portion broadest at upper one-third and bluntly pointed at apex, 6 mm diam. 1 cm from apex; sterile staminate portion 1.2 cm diam.; pistils 2.2 mm long; ovary 5–6-locular, ca. 1.4 mm long, with axile placentation, the sides covered throughout, especially toward apex, with short pale raphide cells; locules 1–1.2 mm long; ovules 20–30 per locule, 0.1–0.2 mm long, oblong, arranged all along the length of the locules; style similar to style type B; short, 0.9–1 mm diam., drying with 2–5 depressions at apex; stigma 1–1.1 mm diam. when flattened and dried. Infructescence not seen.

Flowering in *Philodendron squamipetiolatum* occurs in the rainy season, during June in Central America. Ecuadorian collections at post-anthesis have been seen from February and April, with an early fruiting collection from August.

Philodendron squamipetiolatum ranges from Panama to Ecuador from sea level to 1300 m elevation in *Premontane rain forest* and *Premontane wet forest* transition to *rain forest* and *Tropical rain forest*. In Panama this species is known only from along the Continental Divide in Coclé Province,

whereas in South America it occurs along the Pacific slope of the Andes.

Philodendron squamipetiolatum is a member of *P.* sect. *Philodendron* subsect. *Achyropodium*. This species is distinguished by its long, inconspicuously scaly internodes; long, scaly, terete petioles (hence the name); long, scaly, deciduous cataphylls; rounded to subcordate blades with an arcuate sinus and puberulent major veins below; 1–2 dark green, scaly inflorescences; and spathe tube reddish within.

In Central America, *Philodendron squamipetiolatum* is most easily confused with *P. hammelii*, a species with which it occurs in the vicinity of the type locality. Both species have small, ovate-cordate blades with scaly petioles and persistent, fibrous cataphylls. *Philodendron hammelii* is distinguished by having leaves drying grayish green above and yellowish brown below and closely arranged broad scales only near the apex of the petioles.

This species might also be confused with two others with scaly petioles. It is easily distinguished from both *P. verrucosum* and *P. squamicaule* by its much smaller, subcordate vs. deeply cordate leaf bases, and from *P. squamicaule* by its more broadly ovate blades (vs. triangular ovate).

Madison & Besse 17185 from Esmeraldas Province, Ecuador, probably also belongs to this species, but field notes indicate that the stems are smooth. Unfortunately, there is no stem with the collection. It is not known whether the intent was to indicate that the stems lacked scales or whether it lacked other features. In addition, the stems were reported to be 10–14 cm long and to 1.5 cm diam.

Additional specimens examined. PANAMA. **Coclé**: Alto Calvario, ca. 4.6 km above El Copé, 800 m, 8°39′N, 80°36′W, *Croat 74857* (AAU, B, CAS, CM, COL, DUKE, F, G, GH, HMNM, K, M, MEXU, MO, NY, PMA, RSA, SCZ, S, TEX, US, VEN); *75098* (MO). **Colón**: Río Guanche, 30–100 m, *Croat 79327* (PMA, MO), *79350* (PMA, SCZ).

COLOMBIA. **Chocó**: Serranía de Baudó, Las Animas–Pato on Río Pato, ca. 4 km SW of Pato, ca. 150 m, 5°30′N, 76°46′W, *Croat 56140* (MO); Serranía de Baudó, Río Pato, 10 km SW of Pato, 5°17′N, 76°45′W, *Croat 56074* (MO); San José del Palmar–Novita, ca. 3 km W of San José del Palmar, 930 m, 4°56′N, 76°29′W, *Croat 56650* (COL, JAUM, MO); Pueblo Rico–Istmina, along Quebrada Antón, 15 km W of Santa Cecila, 240–350 m, 5°20′30″N, 76°13′45″W, *Croat 70972* (MO); 300 m downstream and across the river from Catrú, 50–100 m, *Warner & White 123* (COL). **Valle**: Buenaventura–Cali, Sabaletas, km 29, 25 m, *Killip & Cuatrecasas 38775* (US); 100 m, *Croat 38567* (F, MO); vic. Bajo Calima, <100 m, 4°03′N, 77°08′W, *Croat 70218* (CM, MO, NY); 100 m, *Monsalve 3193* (MO). ECUADOR. **Carchi**: El Pailón, ca. 45 km below Maldonado, 800 m, *Madison & Besse 7185* (SEL); Tulcán Cantón, Awá Reservation, Gualpí Chico area, 1300 m, 0°58′N, 78°16′W, *Hoover et al. 3710* (MO, QCA). **Esmeraldas**: Lita, 550–650 m, *Madison et al. 5057* (SEL); Cerro de Río Bravo de Cayapas, 250 m, 0°41′N, 78°56′W, *Holm-Nielsen et al. 25535* (AAU); 40.1 km W of Lita, 350 m, 0°56′N, 78°40′W, *Croat 72309* (L, MO, QCA, US). **Imbabura**: Lita, 812 m, *D'Arcy 14850* (MO). **Pichincha**: Reserva ENDESA, 9 km N of Km 113 on Quito–Pto. Quito Highway, 750–800 m, 0°05′N, 79°02′W, *Rodríguez 247* (MO, QCA); *Croat & Rodríguez 61483* (MO, QCA); 650–800 m, 0°03′N, 79°07′W, *Cerón & Ayala 10169* (MO); along tributary of Río Guayllabamba, 600 m, 0°10′N, 79°03′W, *Grayum et al. 9353* (MO). **Los Ríos**: La Centinela at Km 12, N of Patricia Pilar, 600 m, *Dodson & Dodson 6771* (MO, SEL); Río Verde, 2 km SE of Sto. Domingo de Los Colorados, 530 m, *Dodson 7435* (SEL).

Philodendron straminicaule Croat, sp. nov. TYPE: Panama. Chiriquí: Fortuna Dam area, trail to meteorological station of Río Hornito, ca. 0.5 km S of Centro de Científicos, 8°45′N, 82°18′W, 23 June 1994, *Croat & Zhu 76302* (holotype, MO–4610957–9; isotypes, AAU, B, CAS, COL, CR, F, GH, K, M, MEXU, NY, PMA, QCNE, S, SEL, US, VEN). Figures 6, 376, 389–392.

Planta hemiepiphytica; internodia 1.5–5(12) cm longa, 2–3.5 cm diam., plus minusve fragilia, canoviridia vel atriviridia, in sicco straminea; cataphylla (17)20–35 cm longa, decidua; petiolus subteres, (27)32–59 cm longus, 5–12(17) mm diam.; lamina triangulari-ovato-cordata, (27)33–55 cm longa, (11)19.7–31 cm lata, cordata basi; inflorescentia 2–3(5); pedunculus (4.5)5.6–18 cm longus; spatha 7–18.5 cm longa; lamina spathae alba in superficiebus ambabus; tubo spathae extus pallide viridi, intus rubroviolaceo vel marronino; pistilla 4–6(10)-locularia; loculi 1-ovulati; baccae virella-albae vel lavandulae.

Hemiepiphytic; stem appressed-climbing, leaf scars conspicuous, 1–1.6 cm long, 1.2–1.7 cm wide; internodes glossy to semiglossy, ± brittle, somewhat scurfy, 1–5(12) cm long, 2–3.5 mm diam., longer than broad, dark green, soon gray-green, finally light tan, drying straw-colored, sometimes with a narrow ring of yellow-brown periderm at the nodes; epidermis transversely fissured in part, sometimes deeply fissured and cracking free on drying; roots blunt, to 30 cm or longer, 4 mm diam., yellow-green, weakly glossy (fresh), drying reddish brown with minute scales in age; cataphylls somewhat spongy, to (17)20–35 cm long, variously ribbed, sometimes D-shaped or unribbed, more frequently bluntly to sharply 1- or 2-ribbed (sometimes unribbed in Coclé), emarginate at apex, pale green to pale yellowish to whitish, margins clear, sometimes closely dark green short-lineate, sometimes moderately red-purple-spotted (more so at base) throughout, ribs darker, drying greenish or brownish, deciduous, persisting intact; **petioles** (27)32–59 cm long, 5–12(17) mm diam., subterete,

± spongy, medium green, obtusely flattened adaxially, rounded abaxially, surface semiglossy, faintly dark lineate; **blades** triangular-ovate-cordate, subcoriaceous, semiglossy, bicolorous, long acuminate at apex, cordate at base, (27)33–55 cm long, (11)19.7–31 cm wide (1.3–2.3 times longer than wide), (0.7–1.5 times longer than petiole), margins hyaline, lower surface drying green to yellow-green, densely glaucous with secretory ducts visible; anterior lobe (18.7)27–38.6(47) cm long, 17.6–27.6 cm wide (2.4–4.5 times longer than posterior lobes), margins straight to moderately concave; posterior lobes directed toward base, rarely reflexed-spreading, sometimes overlapping when posterior lobes are held somewhat upward at an angle to the midrib, (7)8.5–15.5 cm long, 7.5–13 cm wide, obtuse to rounded; sinus hippocrepiform, rarely closed, 2.6–14 cm deep; midrib flat to broadly rounded, paler than surface above, convex to narrowly rounded, paler than surface below; basal veins 4–6(7) per side, with 0–1 free to base, the remainder coalesced 1.2–5 cm, 2 coalesced 3.5–7 cm; posterior rib naked 0.5–1.5 cm; primary lateral veins 3–6 per side, departing midrib at a 45–65° angle, acutely ascending then weakly arcuate to straight to the margins, ± obscure, sunken and concolorous above, convex, darker than surface or paler than surface below; interprimary veins raised and darker than surface below; minor veins moderately distinct, fine, darker than surface, arising from both the midrib and primary lateral veins, drying minutely granular, prominulous and alternating with secretory ducts. INFLORESCENCES erect, usually 2–3 (sometimes to 5) per axil; peduncle (4.5)5.6–18 cm long, terete, pale to medium green, faintly short-lineate to densely speckled; **spathe** 7–18.5 cm long (0.9–1.8 times longer than peduncle), moderately constricted above the tube; spathe blade pale green to white on both surfaces, acuminate at apex; spathe tube dark green, finely pale lineate, glossy outside, 4–8.5 cm long, 1.5–3 cm diam., reddish violet to maroon or magenta inside; **spadix** sessile; erect at anthesis, 7.6–13 cm long; pistillate portion 2.2–3.7(6.5) cm long, 1–1.4(2) cm diam. at middle, tapered slightly toward both ends; staminate portion clavate, 5.2–7.7 cm long; fertile staminate portion white, 8–10 mm diam. at base, 1–1.5 cm diam. at middle, 4–8 mm diam. ca. 1 cm from apex, broadest at the middle, abruptly tapered toward apex, weakly constricted just above the sterile portion; sterile staminate portion usually broader than the pistillate portion at anthesis, 8–15 mm diam., the lowermost flowers sometimes drying whitened; pistils 1.1–1.7(3.4) mm long, 7–9(17) mm diam.; ovary 4–6(10)-locular, 0.5–0.7(2.2) mm long, 0.7–0.9(1.7) mm diam., with sub-basal placentation; locules 0.5–0.7(2.1) mm long, 0.2–0.3(0.6) mm diam.; ovule sac 0.5–0.7 mm long; ovules 1 per locule, contained within sticky, transparent, gelatinous ovule sac, 0.2–0.3 mm long, as long as funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.5–0.8(1) mm long, 0.6–0.7(1.7) mm diam., drying doughnut-shaped, similar to style type C; style funnel shallow with a small ring of stylar canals near the base; stigma subdiscoid, truncate, 0.4–0.5(0.8) mm diam., 0.1–0.3 mm high, covering almost entire style apex, with 1–5 depressions when dried, papillate, sessile, matte; the androecium truncate, prismatic, margins ± 4–5-sided, 0.6–1 mm long, 1.1–1.3 mm diam. at apex; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another and nearly contiguous to contiguous; pollen ± spheroidal, <0.1 mm long, <0.1 mm diam., scarce; sterile staminate flowers irregularly 4–6-sided, blunt, prismatic, 1–1.3 mm long, 0.9–1.2 mm wide. INFRUCTESCENCE with berries pale green (immature), greenish white to lavender.

Flowering in *Philodendron straminicaule* is believed to occur throughout much of the dry season to the mid-rainy season (January through August) in Panama, but flowering specimens have been seen from only April through August. Post-anthesis inflorescences have been seen from as early as March, and immature fruits as early as February, making it obvious that the plants have to be in flower as early as January. Post-anthesis inflorescences have also been collected from May through September and November, and immature fruits occur in March and July. The post-anthesis inflorescences from November suggest that flowering occurs as late as September or October.

Philodendron straminicaule is known only from the Cordillera de Guanacaste in northwest Costa Rica and in western Panama, from Chiriquí and Bocas del Toro to Coclé Province, at (710)950 to 2200 m elevation, generally in *Tropical Lower Montane rain forest* and *Premontane rain forest*, rarely in *Tropical wet forest.*

Philodendron straminicaule is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species is characterized by its grayish (drying straw-colored), more or less brittle, glossy internodes, which are longer than broad; deciduous cataphylls; obtusely flattened, more or less spongy petioles; and triangular-ovate-cordate, green-drying blades with the lower surface drying densely and minutely granular and secretory ducts usually prominently visible and alternating with the minor veins. Also characteristic is the white spathe blade

and tube green outside and reddish violet to maroon inside.

Philodendron straminicaule is similar to *P. wilburii* var. *longipedunculatum*, but the latter species differs in having longer, more slender internodes; longer, unribbed to bluntly 1-ribbed cataphylls; typically smaller blades that dry brownish with mostly 3–4 primary lateral veins; and especially by having the peduncle usually as long as or even longer than the spathe (vs. usually less than length of spathe). It also differs in having orangish (rather than greenish white to lavender) berries.

The species may be confused with *P. alticola* and *P. smithii*. See those species for separation.

A noteworthy collection is *Croat 66503*, which has the veins on the lower leaf surface drying darker than the surface rather than paler, which is normally the case.

Collections from Costa Rica differ from those in Panama in having slightly smaller leaves with both the petioles and the blades shorter than those in Panama (petioles to 28 cm long and blades to 31 cm long in Costa Rica vs. petioles to 59 cm long and blades to 55 cm long in Panama). Nevertheless, the smaller leaves in Panama range down to only slightly larger than those in Costa Rica (with petioles as short as 32 cm long and blades to as small as 33 cm long).

One collection from Guanacaste (*Herrera 1473*) is unusual in having more narrowly triangular blades with concave margins, narrower posterior lobes, a parabolic sinus, and a D-type style. However, it is otherwise similar, having the same dried stem characteristics and 1 ovule per locule. More collections are needed to determine if this entity is distinct from *P. straminicaule*.

This species perhaps also occurs in Colombia based on collections from Valle Department (*Juncosa 2054*) at 580 m and from Gorgonilla Island, Cauca Department (*Killip & García 33060*). These collections differ from those in Panama in having blades with no obvious secretory ducts visible on the abaxial surface. In addition, the latter collection is from just 130 to 200 m elevation, substantially lower than where it is found in Panama.

Additional specimens examined. COSTA RICA. **Alejuela**: above Bijagua, slopes of Miravalles, *Gómez et al. 19171* (MO). **Guanacaste**: Parque Nacional Guanacaste, Estación Cacao, 1100 m, 10°55′45″N, 85°28′15″W, *Chávez 80* (INBIO, MO); Estación Mengo, 1100 m, 10°55′N, 85°28′W, *INBio 219* (CR, MO); Parque Nacional Rincón de la Vieja, SE slopes of Volcán Santa María, above Estación Hacienda Santa María, 900–1200 m, 10°47′N, 85°18′W, *Davidse et al. 23397* (CR, MEXU, MO, TEX); 1350–1400 m, 10°46′N, 85°49′W, *Herrera 1473* (CR, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, 21.4 km past Gualaca, 8°32′N, 82°19′W, *Hoover 1326* (MO); Continental Divide, 1200 m, 8°44′N, 82°17′W, *Croat 60350* (CM, MO); *60364* (AAU, CM, COL, CR, F, M, MO, PMA, UC, WIS), *60365* (K, MO, PMA, US); 8°45′N, 82°15′W, *McPherson 10867* (CR, MO, PMA); 2.8 mi. from Divide, 850–950 m, ca. 8°45′N, 82°15′W, *9675* (L, MO, PMA, US). **Bocas del Toro–Chiriquí**: Fortuna Dam area, Continental Divide, above Quebrada Arena, road to Oleoducto, 1150–1200 m, *Knapp & Vodicka 5658* (MO, PMA). **Chiriquí**: Cerro Colorado, above San Félix, 18–27 mi. off of Pan-American Highway, 1200–1500 m, *Croat 33146* (MO); 19.7 mi. N of Río San Félix, 1420 m, 8°31′N, 81°46′W, *Croat 74996* (MO); 33.1 km N of Río San Félix, ca. 1400 m, *Croat 37203* (MO, PMA); 20 mi. N of Río San Félix, 2000 m, *Croat 48446* (COL, K, MEXU, MO, PMA, VEN, W); 1420 m, *75010* (MO, PMA); vic. of Chame, 800–1200 m, *Croat 33440* (MO); 11.2 km from Chame, 1700 m, *Folsom 4889* (CAS, MO); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69013* (B, CAS, CM, COL, CR, F, G, K, L, MEXU, MO, PMA, TEX, US); Cerro Horqueta, 7000 ft., *Blum & Dwyer 2591* (SCZ); Boquete, 5000–6000 ft., *Dwyer & Hayden 7736* (MO); 6500 ft., *von Hagen & Von Hagen 2073* (MO, NY); *2164* (MO, NY); Volcán Barú, along old road to Boquete, 1750–1900 m, 8°50′N, 82°30′W, *McPherson 11340* (K, MO); Cerro Pate Macho, ca. 5 mi. NE of Boquete, 1800–2200 m, *Croat 48562* (MO); 1900–2000 m, 8°46′N, 82°25′W, *66503* (MO); ca. 6 km NE of Boquete, 8°49′N, 82°23′W, *Grayum 6408* (CM, MO, PMA); 1600-1700 m, *Grayum et al. 6397* (MO, US); Río Palo Alto, 1300–1800 m, 8°47′N, 82°22′W, *Knapp et al. 2042* (MO); Fortuna Lake area, Gualaca–Chiriquí Grande, along Continental Divide, 1200 m, 8°44′N, 81°17′W, *Croat 74972* (MO, PMA); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60057* (AAU, B, CAS, F, K, L, MEXU, MO, PMA, SEL, U); ca. 4.6 mi. N of Los Planes de Hornito, *Stevens 18437* (MO); behind Vivero Forestal (now Centro de Científicos), 12 km N of Los Planes de Hornito, 1200–1300 m, 8°45′N, 82°12′W, *Knapp 4950* (MO); 10.1 mi. NW of Los Planes de Hornito, 1250 m, 82°17′W, 8°45′N, *Croat 49837* (BR, COL, MO, NY, TEX, UC), *50030* (MO, NY, TEX); vic. IRHE facilities, 1100–1200 m, 8°45′N, 81°18′W, *Croat 66542* (MO, PMA), *66584* (AAU, BR, CAS, CDBI, CM, DUKE, F, IBE, K, KYO, LE, MBM, MEXU, MO, NY, PE, PMA, RB, SCZ, UC, US); Río Chiriquí, 9.6 mi. beyond Los Planes de Hornito, 1300 m, *Croat 48733* (CR, MO); 11.8 mi. NW, 1400 m, *48686* (MO), *48703* (CM, MO), *48701* (CAS, MO); Quebrada Bonita, 1100 m, 8°45′N, 82°13′W, *Churchill 5262* (MO); Quebrada Ortega, 1200 m, 8°41′N, 82°14′W, *Churchill 5283* (MO); 8 mi. beyond Los Planes de Hornito, 1010–1130 m, 8°44′N, 82°14′30″W, *Croat 67920* (AAU, CAS, MO, PMA, US). **Coclé**: El Copé region, Alto Calvario, ca. 6 km N of El Copé, 770 m, 8°38′N, 80°35′W, *Croat & Zhu 76761* (MO, PMA); 710–800 m, 8°39′N, 80°36′W, *Croat 68816* (MO); 900 m, *44576* (MO); 5.5 mi. N of El Copé, 850 m, 8°39′N, 80°36′W, *67574* (CM, MO, PMA, TEX). **Veraguas**: Santa Fe region, Escuela Agrícola Alto Piedra, ca. 5–8 km NE of school, 730–770 m, *Croat 25909* (MO, NY).

Philodendron strictum G. S. Bunting, Phytologia 60: 328. 1986. TYPE: Venezuela. Táchira: San Cristóbal–Chorro del Indio–Caño Seco–La Florida, km 20–22 (E of San Cristóbal), 1100–1125 m, 6 Mar. 1977, *Bunting & Borges 5001* (holotype, NY; isotypes, PT, VEN). Figures 393–395, 397, 398.

Terrestrial or hemiepiphytic; stems stout; internodes 3–4 cm long, 2.5–5 cm diam., usually broader than long, sometimes longer than broad, dark green to gray-green, semiglossy; roots moderately few, drying dark brown, semiglossy, sparsely scaly; cataphylls 25–40 cm long, unribbed to bluntly 1-ribbed, rarely bluntly 2-ribbed or sharply 1-ribbed, pale green, soft, turning yellowish and persisting semi-intact at upper nodes; **petioles** (47–56)63–105 cm long, subterete, obtusely D-shaped with faint medial rib, obtusely flattened adaxially, light green to gray-green, weakly glossy, sparsely dark lineate, drying usually light yellow-brown, sometimes blackened; sheath inconspicuous; **blades** ovate-cordate, conspicuously bicolorous, acuminate at apex (the acumen sometimes inrolled), cordate, sometimes sagittate at base, (24)38–66(74) cm long, (16)27–52 cm wide (1–1.3 times longer than wide), (0.5–1 times the petiole length), broadest near the middle; upper surface dark green, semiglossy, lower surface much paler, whitish, matte; anterior lobe (19–28)31–51(57–62) cm long, (19)27–48(53–56) cm wide, (1.7–2.8(3.3) times longer than posterior lobes); posterior lobes 12–23 cm long, 8.6–26 cm wide, obtuse to broadly rounded; sinus usually spathulate, sometimes hippocrepiform; midrib flat, paler than surface above, convex and darker below; basal veins 7–10 per side, with 0–2 free to base, part of the remainder coalesced 1–12.4 cm; posterior rib sometimes not naked, often obscurely naked for 1.5 cm, rarely 3.5 cm; primary lateral veins 5–11 per side, departing midrib at a 50–65° angle, deeply sunken above, convex and darker below, usually prominently downturned before meeting midrib; minor veins numerous, fine, indistinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect-spreading, 1–4 or more per axil; peduncle (6)11–15 cm long, 1–1.5 cm diam., with thin, yellowish epidermis; **spathe** 13–17.7 cm long, 2.5–4.3 cm diam. (0.9–2.3 times longer than peduncle), moderately constricted above the tube (very slick inside), 2.7 cm diam. at constriction; spathe blade light green to whitish, tinged purple-violet (B & K red-purple 3/2.5), sparsely short-white-lineate medially outside, margins paler, (opening elliptic in face view, 10.7 cm long, 4.8 cm wide), light green to whitish and suffused red inside, drying dark to reddish brown; spathe tube green to purple-violet (B & K red-purple 3/2.5) outside, 4 cm diam., maroon or violet-purple inside; **spadix** sessile; bluntly pointed at apex, 9.2–16 cm long; pistillate portion weakly tapered toward apex, 2.1–3.9 cm long in front, (1.6)3–3.3 cm long in back, 0.6–1.4 cm diam. at apex, 1–1.5 cm diam. at middle, 1.3–1.5 cm wide at base; staminate portion 8.9–11.9 cm long; fertile staminate portion somewhat ellipsoid, sometimes ovate to tapered, 1.1 cm diam. at base, 1.2–1.3 cm diam. at middle, 8–9 mm diam. ca. 1 cm from apex, broadest in the middle or sometimes just above the base, narrower than the pistillate portion, as broad as the sterile portion; sterile staminate portion narrower than the pistillate portion, 1–1.4 cm diam.; pistils (1.1)2.7–3.4(5.4) mm long, 1.3–1.6 mm diam.; ovary (4)5–6-locular, 1.8 mm long, 1.3–1.7 mm diam., with axile placentation; locules 1.8 mm long, 0.6 mm diam.; ovules 20–28 per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle; funicle 0.1 mm long, adnate to lower part of partition, style 0.7–0.9 mm long, 1.3–1.6 mm diam., similar to style type B; style apex flat; stigma subdiscoid, truncate, 1.1–1.3 mm diam., 0.3–0.5 mm high, covering entire style apex; the androecium prismatic, truncate, oblong, irregularly 4–6-sided at apex 0.9 mm long, 1.6–2 mm diam. at apex; thecae oblong, ± parallel to one another, nearly contiguous; sterile staminate flowers blunt, prismatic, irregularly 4–6-sided, 1.8–2.9 mm long, 0.9–2.4 mm wide. INFRUCTESCENCE 2 cm wide; seeds pale yellowish, 0.9 mm long, 0.3 mm diam.

Flowering in *Philodendron strictum* apparently occurs throughout the dry season and first half of the rainy season in Central America (January through September, though no flowers were seen in May). South American flowering collections have been seen from February and July, and post-anthesis inflorescences (or immature fruits) from January through November. Mature fruits have been seen only from September.

Philodendron strictum ranges from Costa Rica to western Panama, Venezuela (Táchira), Colombia (Antioquia, Chocó), and Ecuador (Carchi, Esmeraldas). In Costa Rica, this species occurs at 850 to 1525 m, and in Panama at 680 to 1665 m elevation in *Lower Montane rain*, *Premontane rain*, and *Tropical wet forest* life zones. In Colombia, this species has been collected at 100 to 150 m in Chocó and Valle Departments, and in Antioquia at 1560 m. In Venezuela, it is known only from the state of Táchira in the southwestern part of the country, at 1000 to 1250 m elevation in *Premontane wet forest*. It was reported erroneously (owing to a typographical error) by Croat and Lambert (1986) from 110 to 1330 m.

Philodendron strictum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Impolita*. This species is characterized by its usually terrestrial habit; thick stems; short internodes; thick, yel-

lowish, unribbed to bluntly one-ribbed cataphylls persisting semi-intact at the upper nodes; obtusely flattened to D-shaped petioles usually drying pale yellow-brown; and ovate-cordate blades with the lower surface whitish and matte.

Philodendron strictum is most easily confused with *P. hebetatum*, which shares blades with whitish, matte lower surfaces, as well as yellow-drying cataphylls and petioles. Both species are easily identified by these features alone. The two species are sympatric in at least one area along the Fortuna Dam road in Panama but remain distinct by virtue of their respective habits and blade shapes. *Philodendron hebetatum* differs in being consistently an appressed epiphyte and in having a triangular-ovate blade vs. a generally terrestrial habit and consistently ovate blades for *P. strictum*. Juvenile plants of the two species, at this stage both terrestrial, are quite distinct with the blades of *P. hebetatum* more elongate (2.5–3 times longer than broad), while those of *P. strictum* are more broadly ovate (1.2–2.5 times longer than wide).

This species is also easily confused with the often syntypic *P. thalassicum*, which differs in having blackened rather than pale yellow-brown petioles, cataphylls promptly weathering to pale fibers vs. usually persisting yellowish and semi-intact in *P. strictum* and internally greenish to white spathes (vs. maroon or violet-purple in *P. strictum*). In addition (at least in Panama), the petioles of *P. thalassicum* are more sharply D-shaped vs. obtusely flattened in *P. strictum*.

A collection from 1875 m elevation in Antioquia Department, Colombia (*McPherson 12939*), possibly belongs to this species but differs in having reddish brown cataphylls that are more fragmented on drying. It also has the petioles drying dark brown, not yellowish as is typical for the species in Colombia and Ecuador.

Additional specimens examined. COSTA RICA. **Alajuela**: San Ramón, Bajo Rodríguez, 1025–1100 m, *Croat 78888* (CR, INB, MO). **Cartago**: ca. 11 mi. NE of Turrialba, 850 m, *Croat 43354* (MO); Turrialba–Limón, Hwy. 32, ca. 11 mi. S of Siquirres, 650 m, *Croat 43335* (MO); 31 km S of Siquirres on road to Turrialba (CR-10), 850 m, 9°57′N, 83°36′W, *Thompson & Rawlins 1167* (CM); Shipirí, Moravia de Chirripó, 900–1000 m, *I. Chacón 9* (MO); Tapantí, *Nilsson & Chacon 236* (CR); *Croat 79039* (MO). **Puntarenas**: ca. 1 km S of San Vito, 1100 m, *Croat 66168* (CR, G, MO, NY, PMA); Las Cruces, near San Vito de Java, ca. 4000 ft., *Croat 32959* (MO); N of Palmar Norte, trail to Jalisco, 50–700 m, *Croat 35208* (MO). **San José**: San Isidro de El General–Dominical, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35250* (MO); 990–1100 m, *Croat & Hannon 79105* (CR, INB, MO); Braulio Carrillo National Park, 1400 m, *Croat 78811* (CR, INB, MO); Tarrazu, vic. Hormiguero, 1100-1200 m, *Croat 78939* (CR, INB, MO). PANAMA. **Bocas del Toro**: Fortuna Dam area, Continental Divide, 1170 m, 8°44′N, 82°17′W, *Croat 66649* (AAU, B, CAS, CM, COL, CR, F, G, K, L, MEXU, MO, NY, PMA, US, VEN); 1000 m, 8°48′N, 82°12′W, *Churchill et al. 4646* (MO); ca. 1200 m, 8°44′N, 82°17′W, *Croat & Grayum 60326* (B, CM, K, MO, RSA, US); 2.2 mi. N of Continental Divide, 820 m, 8°45′N, 82°16′W, *Croat 60401* (MO); 825 m, 8°45′N, 82°15′W, *McPherson 7361* (B, K, MO, PMA, RSA); 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60475* (MO, PMA). **Chiriquí**: Cerro Colorado, 9–10 mi. road to Chame, 1200–1500 m, *Croat 33272* (MO); 7.7 mi. beyond Chame, 1420 m, 8°31′N, 81°46′W, *74995* (MO); Chame, 1600 m, *Kress et al. 86-1925* (SEL); 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69064* (MO); 6.5 km beyond Chame, 1660 m, 8°30′N, 81°46′W, *Croat 74991* (MO); Fortuna Dam area, Gualaca–Chiriquí, 1200 m, 8°46′N, 82°16′W, *Croat 68030* (F, MO); E of main camp at dam site, 1400–1500 m, *Folsom et al. 5448* (MO); trail to Río Hornito weather station, 1100–1200 m, 8°45′N, 82°15′W, *Thompson 5041* (CM); 8°45′N, 82°18′W, *Croat & Zhu 76311* (AAU, CM, COL, CR, DUKE, EAP, GH, IBE, MEXU, MO, P, QCNE, RSA, US); *76375* (CAS, CM, COL, CR, DUKE, ENCB, F, GB, K, L, MEXU, MO, NY, P, SEL, WIS); Continental Divide, 1200 m, 8°44′N, 81°17′W, *Croat 74971* (MO, PMA); Quebrada Arena, just S of Continental Divide, 1050 m, 8°45′N, 82°16′W, *Hammel et al. 14707* (MO); Quebrada Los Chorros–Quebrada Honda, to N of reservoir, 8°45′N, 82°14′W, *H. Churchill & A. Churchill 6166* (MO, NY); vic. IRHE facilities at dam, 1200–1300 m, 8°45′N, 82°18′W, *Croat 66543* (AAU, DUKE, F, M, MEXU, MO, PMA); Gualaca–Chiriquí Grande, 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *Croat 67840* (CM, MO, PMA); 8.4 mi. beyond Los Planes de Hornito, 1130 m, 8°44′N, 82°14′35″W, *67870* (G, M, MO). **Coclé**: El Copé region, Alto Calvario, ca. 6 km N of El Copé, 8°39′N, 80°36′W, *Croat 68818* (MO); 680–770 m, 8°39′N, 80°36′W, *74852* (MO, W); 700 m, 8°38′N, 80°35′W, *Croat & Zhu 76796* (MO, NY); El Valle region, vic. of La Mesa, N of El Valle de Antón, Cerro Gaital, 900–1000 m, 8°37′N, 80°08′W, *Croat 67227* (B, CAS, CM, K, MO). **Veraguas**: Santa Fe region, Alto de Piedra, 800–950 m, 8°33′N, 81°08′W, *Croat 67003* (CAS, MO); Parque Nacional Cerro Tute, 0.5 mi. N of Alto Piedra, 800–1030 m, *Croat & Zhu 76885* (MO); 1000–1250 m, *Croat 48920* (MO).

Philodendron subincisum Schott, Oesterr. Bot. Z. 9: 99. 1859. TYPE: Mexico. Veracruz: Papantla, 20°27′N, 97°19′W, *Karwinski s.n.* (holotype, LE? destroyed?); Schott ic. 2636 (neotype, here designated, W). Figures 396, 401, 402.

Hemiepiphytic; leaf scars conspicuous, 1–1.5 cm long, 1–2 cm wide; internodes 1.2–6 cm long, 2.7–3 cm diam., broader than long, tan to reddish brown, epidermis with loose flakes; roots few to numerous per node; cataphylls moderately spongy, 23–34 cm long, unribbed, drying sharply 1-ribbed in lower one-third, pale green, drying tan to reddish brown, persisting semi-intact, eventually fibrous; **petioles** 55.5–68 cm long, 1.4–1.5 cm diam., terete, medium green, drying yellowish tan to reddish

tan, surface dark green diffuse-lineate; **blades** narrowly ovate, coriaceous, semiglossy, moderately bicolorous, long acuminate at apex, sagittate at base, (40)57.5–72 cm long, (24)32.5–37 cm wide (1.7–1.8 times longer than wide), (ca. 1 time longer than petiole), margins hyaline, markedly sinuate, upper surface drying brown, lower surface drying yellow-red to brown; anterior lobe (32.5)40–49 cm long, (10)17.6–18 cm wide (2.3–3.3 times longer than posterior lobes); posterior lobes (10)17–18 cm long, 16–16.5 cm wide, obtuse; sinus hippocrepiform or closed and obovate with lobes overlapping, acute when young; midrib broad, flat, paler than surface above, convex, concolorous below; basal veins 4–9 per side, first (second) pair free to base, most coalesced 1–4 cm, 2–3 coalesced to 5.5 cm; posterior rib not naked or obscurely naked for ca. 1 cm; primary lateral veins 5–7 per side, departing midrib at a 50–60° angle, sunken, paler than surface above, convex, concolorous below; minor veins flat, darker than surface below, arising from both the midrib and primary lateral veins. INFLORESCENCES 2 per axil, ± erect; peduncle 7.5–10 cm long, 1.3 cm diam., medium green; **spathe** 16.5–20 cm long, 3.5 cm diam. (closed), 5 cm diam. (opened), constricted above the tube, acuminate at apex, margins paler; spathe blade semiglossy, greenish outside, white inside; spathe tube more ellipsoid, maroon-purple outside, bright cherry-red inside; **spadix** not seen.

The flowering phenology of *Philodendron subincisum* is unknown. The only modern collection (*Moore & Bunting 8952*) is sterile.

Philodendron subincisum is endemic to Mexico, known only from northern Veracruz in the Poza Rica region, at less than 500 m elevation in "Selva Mediana Subperennifolia."

Philodendron subincisum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is characterized by its large, thick stems, short internodes, deciduous cataphylls, subterete petioles, ovate-cordate blades with markedly sinuate margins, two short-pedunculate inflorescences per axil, spathe tube maroon-purple outside and bright cherry-red inside, and spathe blade green outside and white within.

Philodendron subincisum is apparently rare, having been collected only once (*Moore & Bunting 8952*) since the type gathering.

Philodendron subincisum appears to be most closely related to *P. sagittifolium* based on most features, but it may represent a hybrid. Bunting (1965) even suggested that *P. radiatum* was closely allied to *P. subincisum*. Judging from its rarity, the latter taxon might be a hybrid between *P. radiatum* and *P. sagittifolium*. Because of its ovate blade with sinuate margins, it is not confused with either of the above species. Perhaps most easily confused with *P. subincisum* is *P. radiatum* var. *pseudoradiatum*. That taxon differs in occurring only on the Pacific slope and in having ovate-triangular blades with proportionately narrower and longer lobes.

The inflorescence of this species remains poorly known. Collected in sterile condition by Moore and Bunting (*8956*), the species later flowered in cultivation at Cornell University. The flowering specimen was apparently vouchered by Bunting, but the whereabouts of the collection are unknown. Much of the information concerning the species is based on photographs published by Bunting (1965).

Additional specimen examined. MEXICO. **Veracruz**: Rancho El Huasteco, 14.6 mi. from Tuxpan on road to Tihuatlán, *Moore & Bunting 8956* (BH, MO).

Philodendron sulcicaule Croat & Grayum, sp. nov. TYPE: Costa Rica. Limón: 7 km SW of Bribrí, 100–250 m, ca. 9°36'N, 82°54'W, 4 May 1983, *Gómez, Liesner & Judziewicz 20473* (holotype, MO–3160203; isotypes, B, CR, K, PMA, US). Figures 399, 400, 403.

Planta hemiepiphytica; internodia 6–16 cm longa, 5–13 mm diam., profunde sulcata; cataphylla 12 cm longa, incostata, vel acute 1-costata, raro acute 2-costata, deciduа intacta; petiolus 11–20 cm longus, subteres, leniter complanatus adaxialiter; lamina ovato-cordata, abrupte vel longa acuminata, 14.5–24 cm longa, 9.6–15 cm lata; nervis basalibus 3 utroque, infirmis; nervis lateralibus 1 obscuris; inflorescentia 1–4(5); pedunculus tenuis, 3.5–10 cm longus, 1–3 mm diam.; spatha (4.5)5.8–11 cm longa, omnino alba, tubo spathae intus rubro, roseo aut purpureo basi; pistilla 4–5-locularia; loculi 1-ovulati.

Hemiepiphytic vine; stem scandent, drying yellow, glossy; internodes deeply sulcate, prominently ribbed, semiglossy, 6–16 cm long, 5–13 mm diam., longer than broad, olive-green; epidermis becoming brown, breaking free on bending stem; roots red-brown, slender, curled, 8–20 cm long; cataphylls 12 cm long, unribbed to sharply 1-ribbed, rarely sharply 2-ribbed, green rarely pink, deciduous intact; **petioles** 11–20 cm long, 4–8 mm diam., subterete, dark green, weakly flattened adaxially, semiglossy; **blades** ovate-cordate, subcoriaceous, semiglossy, moderately bicolorous, abruptly- to long-acuminate at apex (the acumen apiculate, to 4 mm long), cordate at base, 14.5–24 cm long, 9.6–15 cm wide (1.3–1.9 times longer than wide), (0.9–1.6 times longer than petiole), about two-thirds as long as petiole, margins drying moderately undulate, upper surface dark green, drying usually

dark brown, semiglossy to matte, lower surface paler, drying light brown to greenish brown, sometimes yellowish brown, semiglossy; anterior lobe 10–19.6 cm long, 7–15 cm wide (2.6–3.8 times longer than posterior lobes); posterior lobes 3.5–6 cm long, 2.7–6.4 cm wide, rounded-obtuse to nearly acute; sinus arcuate with blade decurrent on petiole to short-hippocrepiform; midrib flat to weakly raised, concolorous above, convex, concolorous to paler than surface below; basal veins to 3 per side, weak, 1 sometimes free to base, the remainder coalesced 0.5–2 cm; posterior rib naked for all its length; primary lateral veins obscure above, obscure below; minor veins distinct, fine, close, arising from the midrib only; "cross-veins" sometimes visible. INFLORESCENCES 1–4(5) per axil; peduncle 3.5–10 cm long, 1–3 mm diam., reddish, whitish or purplish, slender; **spathe** (4.5)5.8–11 cm long, (0.9–1.1(2) times longer than peduncle), weakly constricted midway, 5 mm diam. at constriction, white throughout, becoming greenish (post-anthesis), rarely reddish (*Gómez et al. 20473*), cuspidate-acuminate at apex (the acumen ca. 1.5 mm long), white inside; resin canals appearing as intermittent lines in lower two-thirds of spathe, extending into upper part of spathe tube, drying blackened; spathe tube 3–4 cm long, red, pink, or purple at base inside; **spadix** sessile; slender, acute at apex, 4.5–7.7 cm long, broadest at the middle of the staminate portion, constricted scarcely or not at all above the sterile staminate portion; pistillate portion white, 2.5 cm long, 4.5 mm diam. midway, 3.5–4.5 mm diam. at apex and at base; staminate portion 3–5.2 cm long; sterile staminate portion cream, 3–4 mm diam.; pistils white; ovary 4–5-locular, with ± subbasal placentation; locules 0.4 mm long, 0.2–0.3 mm diam.; ovule sac 0.4 mm long; ovules 1 per locule, contained within translucent or transparent ovule sac, 0.2–0.3 mm long; funicle 0.1–0.2 mm long (can be pulled free to base), style similar to style type B; style apex flat; stigma subdiscoid, unlobed, ± truncate, 0.4–0.5 mm diam., 0.1 mm high, covering center of style apex; the androecium margins irregularly 4–6-sided, 0.6–1.2 mm long. INFRUCTESCENCE peduncle, 8 cm long, 1 cm diam.

Flowering in *Philodendron sulcicaule* occurs during the dry season and early wet season (December through May, though no flowering collections have been seen from April). Post-anthesis collections have been seen from March and April. No fruits have been seen.

Philodendron sulcicaule ranges from extreme southeastern Costa Rica to the Atlantic slope of Panama, from 100 to about 700 m elevation (though generally less than 300 m) in *Premontane wet forest* transition to *Tropical wet forest* life zones.

Philodendron sulcicaule is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata*. The species is characterized by its scandent habit; deeply sulcate stems drying yellow and glossy; unribbed, deciduous cataphylls; subterete petioles weakly flattened adaxially; and ovate-cordate blades with obscure primary lateral veins and up to four pairs of weak basal veins. Also characteristic are the numerous (up to five per axil), small, slenderly pedunculate inflorescences with spathes white outside (sometimes tinged red) and red to purplish in the base of the tube.

Philodendron sulcicaule appears closest to an undescribed species from Bajo Calima, Valle Department, Colombia (e.g., *Croat 70137*). Though the latter species has the same habit, petiole shape, leaf size and shape, and ribbed yellowish stems, it differs in having white cataphylls, usually 3–4 primary lateral leaf veins, and 3–5 basal veins with a well-developed posterior rib. In addition, the spathe tube is reddish outside and the entire inner surface is creamy-white (vs. usually white outside and reddish to purplish inside the tube in *P. sulcicaule*).

In Central America, *Philodendron sulcicaule* resembles *P. purpureoviride* and *P. microstictum*, both of which are vines with similar leaves. *Philodendron purpureoviride* differs in having solitary, stout inflorescences (instead with up to three or four smaller inflorescences) and leaf blades with distinct primary lateral veins. *Philodendron microstictum* differs in having blades broader than long (vs. longer than broad in *P. sulcicaule*).

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Chiriquí Grande–Fortuna, 3.2 mi. N of Continental Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60249* (MO). **Coclé**: Bismarck, 2000–3000 ft., *Williams 628* (NY); 16.7 km N of turnoff to Coclesito from Llano Grande, 700 ft., *Hammel 1791* (MO). **Colón**: Santa Rita Ridge Road, ca. 22 km from Transistmian Highway, 500 m, 9°25′N, 79°40′W, *Hammel et al. 14504* (B, CAS, K, MO, PMA, US); E Santa Rita Ridge, *Correa 670* (MO, PMA); Río Iguanita, ca. 1 mi. upstream, *Kennedy & Dressler 3481* (F); Sabanitas–Portobello, Río Piedras Lumber Road, 250 m, 9°22′30″N, 79°41′30″W, *Croat 75167* (CM, MO, PMA, US); Río Guanche, 30–100 m, *Croat 79344* (PMA, MO). **Panamá**: El Llano–Cartí, 12–16 km N of Pan-American Highway, 150–400 m, *Kennedy et al. 3162* (MO); Mile 10, 330 m, *Croat 33734* (CM, F, MO); Mile 12, 200–500 m, *Liesner 1154* (MO, US); ca. 4.6 mi. N, ca. 350 m, 9°15′N, 79°W, *McPherson & Merello 8163* (B, F, MO); Mile 4, 500 m, *Croat 49140* (MO). **San Blas**: El Llano–Cartí road, Mile 12, ca. 1000 ft., *Antonio 3781* (MO); Mile 14, 300 m, 9°15′N, 79°W, *Croat 69246* (CAS, CM, CR, L, MO, NY); Mile 9, 350 m, 9°20′N,

79°W, *Croat & Zhu 76565* (MO). **San Blas–Panamá**: Kuna Divide trail, W of El Llano–Cartí Road, 250 m, 9°20′N, 79°W, *McPherson 11868* (MO); Cordillera de San Blas, Pacific slope headwaters of Río Piria, 200–400 m, 9°12′N, 78°16′W, *H. Herrera et al. 1143* (K, MO, PMA, US).

Philodendron tenue K. Koch & Augustin, in A. Braun et al., Append. gen. sp. Hort. berol. 1854: 7. 1854–1855. TYPE: Cultivated at Berlin, origin unknown (holotype, B? lost); Schott ic. 2465 and 2466 (neotype, here designated, W). Figures 404–407, 413, 414.

Philodendron gracile Schott, Prod. syst. Aroid. 244. 1860. TYPE: Costa Rica. *Wendland s.n.*, not seen (holotype, W? now lost; impression of type is at K); Schott ic. 2687–2688 (neotype, here designated).

Philodendron ecuadorense Engl., Bot. Jahrb. Syst. 26: 531. 1899. TYPE: Ecuador. Manabí, *Eggers 15221* (holotype, B; isotype, F).

Philodendron sodiroanum Engl., Bot. Jahrb. Syst. 26: 531. 1899. TYPE: Ecuador. Pichincha: Nanegal, *Sodiro 47* (holotype, B).

Usually hemiepiphytic, rarely terrestrial or epilithic; stem usually appressed-climbing, thick, short, leaf scars inconspicuous; internodes striate, 2–3.5 cm long, 1–2.5 cm diam., about as long as broad, dark green to olive-green; roots drying tan to brownish red to blackish, smooth, elongate, 7–28 cm long, 0.2–0.5 cm diam., usually few per node, rarely numerous per node, dense, spreading at the nodes, epidermis peeling; cataphylls membranous, 28–31 cm long, 8 cm broad at base, usually unribbed, sometimes bluntly or sharply 1-ribbed to sharply 2-ribbed, green, red or purplish green, pale white-striate, drying brownish to reddish brown, persisting intact, eventually fibrous. LEAVES ± erect; **petioles** 29–107 cm long, 2–11 mm diam., erect, ± terete, stiff, firm, dark green, sometimes somewhat flattened with a low medial rib adaxially, surface weakly semiglossy, weakly light green striate with many small, fine ridges; geniculum thicker than petiole, 3–4 cm long, scurfy, slightly paler than petiole; **blades** ovate to ovate-triangular with prominent posterior lobes, chartaceous to subcoriaceous, moderately bicolorous, narrowly acuminate, sometimes long-acuminate at apex (the acumen inrolled, 1–4 mm long), cordate at base, 31–78 cm long, 16–52 cm wide (1.2–3.1 times longer than wide), (0.6–1.4 times longer than petiole), margins weakly undulate, upper surface gray-green to dark green, glossy, lower surface semiglossy, paler; anterior lobe 30.5–60 cm long, 14–34 cm wide (1.5–3.8 times longer than posterior lobes), broadest at point of petiole attachment; posterior lobes 10–29.5 cm long, 6–16.5 cm wide, broadest at or near the middle, directed downward and outward, sometimes inward, obtuse to subrounded to bluntly acute; sinus triangular, acute to almost obtuse, sometimes closed, 4.5–17 cm deep; midrib flat to sunken, concolorous to slightly paler than surface above, raised, concolorous, drying somewhat paler than surface below; basal veins 5–7 per side, with 0(1) free to base, part of the remainder coalesced 2–10.5 cm; posterior rib not naked; primary lateral veins (6)8–14(20) per side, departing midrib at a 65–90° angle, ± straight or weakly arcuate to the margins, prominently to narrowly sunken above, raised to convex below; interprimary veins as conspicuous as primary lateral veins, weakly sunken and concolorous above, weakly raised and concolorous below; minor veins moderately visible to distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, to 4 per axil; peduncle 2–11 cm long, 3–18 mm diam., pale green, drying reddish brown, heavily white-lineate, drying longitudinally fissured; **spathe** erect to erect-spreading, coriaceous, acuminate at apex, 7–14 cm long, (1.3–4.4 times longer than peduncle), moderately constricted above the tube, 2.1 cm diam. at constriction, short-lineate throughout; spathe blade weakly lanceolate, greenish white, sometimes heavily tinged red outside, 4–8 cm long, 2.1 cm diam., (opening 3.6 cm long), white to pale green inside; spathe tube ovoid, medium to dark green, usually tinged red or sometimes dark violet outside, white-striate with clear margins in front, short, pale green lineate in back outside, 3–7 cm long, 2–3.5 cm diam., white to pale green, sometimes red at base inside, sometimes sparsely white-spotted; **spadix** sessile; 6–12 cm long; pistillate portion yellowish green to pale green, weakly tapered upward, 2.8–4 cm long in front, 1.9–2.2 cm long in back, 1.1–1.6 cm diam. at middle, 1.75 cm wide at base, 0.9–1.5 cm ca. 1 cm from apex, with 12–14 flowers per spiral; staminate portion 5.3–7.1 cm long; fertile staminate portion white, drying orange reddish to light reddish, 1–1.1 cm diam. at base, 1.2–1.5 cm diam. at middle, 7–10 mm diam. ca. 1 cm from apex, broadest in the middle, as broad as to slightly broader than the pistillate portion, as broad as to narrower than the sterile portion, 27–35 flowers visible per spiral; sterile staminate portion as broad as to broader than the pistillate portion, pale brown, 11–17 mm diam.; pistils 2.7–3.1(6.2) mm long, 1.2–1.7(3.9) mm diam.; ovary 4–5-locular, 1.6–2(5.9) mm long, 1.2–1.7(3.9) mm diam., with axile placentation; locules 1.6–2(4.2–5.9) mm long, 0.4–0.7(1.1) mm diam.; ovules 12–14 per locule, 2-seriate, 0.4 mm long, longer than funicle; funicle 0.2(0.5) mm long, adnate to lower part of partition,

style 0.5–0.6 mm long, 1.2–1.7 mm diam., similar to style type B; style apex flat; stigma cupullate, ± hemispheroid, 1.1 mm diam., 0.4–0.6 mm high, covering center of or entire style apex, depressed medially with 6–8 holes; the androecium truncate, prismatic, margins irregularly 4–6-sided, (0.3)0.7–0.9 mm long, 1.1–1.4 mm diam. at apex; thecae oblong, 0.3–0.4 mm wide, ± parallel to one another, nearly contiguous; sterile staminate flowers irregularly 4–6-sided, mostly prismatic, sometimes clavate, blunt, 1.3–2.5 mm long, 1.4–2.5 mm wide. INFRUCTESCENCE with fruits purplish.

Flowering in *Philodendron tenue* occurs during the dry season and early rainy season (January through August, perhaps especially April and May). Post-anthesis collections are from January to October, and immature fruits are known from April through November.

Philodendron tenue ranges from Nicaragua to southern Ecuador (El Oro) on the Pacific slope, and in Venezuela along the foothills of the Sierra de Perijá (Zulia), through the Cordillera de la Costa (Yaracuy to the Distrito Federal at Cerro Naiguatá) and in the foothills of the Cordillera de Mérida south to Apure. In Central America it ranges from 20 to 1400 m in elevation in *Premontane wet forest*, rarely in *Tropical moist forest*. In Colombia it has been collected to 2300 m, and in Ecuador to 1930 m. *Philodendron tenue* is ecologically quite versatile in South America, where it occurs in *Tropical thorn woodland, Premontane thorn woodland, Tropical dry forest, Tropical moist forest,* and *Premontane wet forest* life zones.

Philodendron tenue is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Fibrosa*. This species is characterized by its epiphytic habit, short internodes, persistent cataphyll fibers, more or less terete petioles (equal to or longer than the blades), and especially by its ovate to ovate-triangular blades with prominent posterior lobes often directed outward, narrow to almost closed V-shaped sinus with the posterior ribs not at all naked, and anterior lobe with numerous close primary lateral veins.

Philodendron tenue is similar and perhaps related to *P. maguirei* G. S. Bunting, but that species is terrestrial, has fewer primary lateral veins (typically 3–6 vs. 8–20 for *P. tenue*), and petioles drying straw-yellow (vs. green to brown for *P. tenue*).

The species can be confused with narrow-leaved epiphytic forms of *P. thalassicum* in Costa Rica, but that species has a somewhat glaucous epidermis on the abaxial blade surface and also uniformly greenish spathes.

It is strange that *P. tenue* is found on both sides of the Andes (an unusual pattern except for the most weedy of species), but still does not extend southward from Venezuela. It should certainly be expected at least in Amazonian Colombia.

Additional specimens examined. COSTA RICA. **Alajuela**: Cañas–Upala, 4 km NNE of Bijagua, ca. 400 m, *Croat 36000* (MO); *36294* (MO); 13.8 km N of Bijagua, 100–150 m, *36450* (MO); 8.5 km NE of Villa Quesada, ca. 600 m, *Croat 46969* (MO); 7.5 km N of Río Balsa, 700–800 m, ca. 10°10–15′N, 84°30–35′W, *Stevens 13861* (MO); 17 km NW of San Ramón, 785 m, 10°14.15′N, 84°33′W, *Croat 68161* (CR, F, M, MO); 3.5–4 mi. W of center of San Ramón, 800 m, *46778* (MO); Río San Rafael, W of La Marina, 500 m, 10°23′N, 84°23′W, *Burger & Stolze 5003* (CR, F, GH, NY, US); *5013* (CR, GH, US); San Carlos–San Pedro, ca. 150 m, *Horich s.n.* (M). **Cartago**: Río Gato, 12 km S of Turrialba by air, 4 km SE of Pejibaye, 700 m, 9°48′N, 83°42′W, *Liesner 14360* (CR, MO); Río Reventazón valley, 3 km SE of Turrialba, 500–600 m, *Holm & Iltis 190* (A, BM, G, GH, U); 525–600 m, 9°54′N, 83°39′W, *Liesner et al. 15340* (CR, MO, WIS); Cartago, 4250 ft., *J. D. Smith 5964* (US). **Guanacaste**: Lake Arenal, 550–850 m, 10°27′N, 84°50′W, *Hammel et al. 15140* (MO); Continental Divide, La Chirripa Ridge, 4 km NE El Dos de Tilarán, 1000 m, 10°25′N, 84°53′W, *Haber et al. 4859* (MO); Río Chiquito, Tilarán–Arenal, Zona Monteverde, 700 m, 10°23′N, 84°51′W, *Haber & Bello 8241* (CR, MO); Río Aguas Verdes, 600 m, *Rivera & Dennis 1050* (CR, INB, MO); Río Negro, 1100 m, *Rivera 718* (CR, INB, MO). **Heredia**: vic. Porto Viejo, near Río Sucio, 20 m, *Croat 35691* (F, MO); Río Peje–Río Sardinalito, Volcán Barva, 700–950 m, 10°17′30″N, 84°04′30″W, *Grayum 6924* (MO); *6886* (CR, MO); La Selva Field Station, ca. 100 m, *Grayum 2626* (DUKE); *2901* (DUKE); Parque Nacional Braulio Carillo, above Río Sucio, 5–600 m, *Pennington et al. 11536* (K). **Limón**: Guápiles, 300–500 m, *Standley 37415* (US); *37451* (US); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8366A* (RSA); *8742* (MO, RSA); W of Guápiles, Quebrada Danta, 360 m, 10°12′N, 83°49′W, *Croat 68427* (MO); Finca Castilla, 30 m, *Dodge & Goerger 9270* (MO); Cerro Coronel, 20–170 m, 10°41′N, 83°38′W, *Stevens 23637* (CR, MO); *24462* (CR, MO); Pococi, Sardinas, 15–20 m, *Araya 510* (CR, INB). **Puntarenas**: Osa Peninsula, 500 m, *G. Herrera 4013* (CR, INB, MO); Chacarita–Rincón de Osa, 10 km W of Chacarita, ca. 100 m, 8°45′N, 83°18′W, *Croat & Grayum 59893* (CR, MO); Piedras Blancas, 3.7 mi. W of Pan-American Highway, 90–105 m, 8°46′N, 83°18′W, *Croat 67698* (CAS, CR, MO); vic. Golfito, 100 m, 8°40′20″N, 83°12′10″W, *Hammel 18399* (CR, MO); 6 km S of San Vito de Java, 3500 ft., *Raven 21882* (BM, CR, DS, F); 4000 ft., *22009* (CR, DS, F, WIS). **San José**: Without locality, *Yeilding 235* (CR, F). HONDURAS. **Gracias a Díos**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9293* (MO, TEFH, UNAH). **Olancho**: Poncaya, *Blackmore & Heath 1994* (BM); Río Olancho, 19 mi. NE of San Esteban, 550 m, 15°29′N, 85°43′W, *Croat & Hannon 64475* (B, MO). NICARAGUA. **Boaco**: Cerro Mombachito, 700–1000 m, *Grijalva & Araquistain 80* (MO). **Chontales**: La Libertad, 500–700 m, *Standley 9056* (F); 4 km NW of Santo Domingo, 280 m, ca. 85°06′W.

12°17′N, *Grijalva 3806* (MO). **Jinotega**: La Salvadora–La Palestina, Hwy. 3, 1100–1150 m, ca. 13°04–05′N, 85°53–54′W, *Stevens & Grijalva 15369* (MO); Río Bocay, Salto Kayaska, 190–340 m, ca. 13°51′N, 85°22′W, *Stevens et al. 16464* (CAS, MO); Caño Litutus, ca. 175 m, ca. 13°58′N, 85°21′W, *Stevens et al. 16665* (MO). **Matagalpa**: NW of Cerro Musún, trail to Paiwás, 800–1200 m, *Araquistain & Moreno 2535* (MO); 300–600 m, *2470* (MO); trail to Paylo, 500–800 m, *2568* (K, MO); Macizos de Peñas Blancas, 1000–1400 m, ca. 13°14–15′N, 85°38–39′W, *Stevens et al. 21074* (MO); Cerro Musún, Río Bilampí, 500–800 m, 13°N, 85°14′W, *Araquistain & Moreno 2351* (MO); NW of Cerro Musún, 4 km SW of Wanawás, 200–500 m, 13°00–01′N, 85°14′W, *2613* (HNMN, MO, NY); Cerro Musún, above Salto Grande of Quebrada Negra, 500 m, *Neill 1817* (MO). **Río San Juan**: El Castillito–Caño de Oro, Gigante, 10 m, 10°43′15″N, 84°54′30″W, *Martínez 2191* (MO); Caño Chontaleño, 20 km NE of El Castillo, 200 m, *Neill & Vincelli 3608* (BM, CAS, MO). **Rivas**: Isla Ometepe, Volcán Maderas, 600–1000 m, 11°26–27′N, 83°31–32′W, *Robleto 1674* (ENCB, MO); 800–1000 m, 11°26′N, 85°29′W, *2065* (MO). **Zelaya**: El Cerro La Pimienta, ca. 800–1000 m, 13°44′50″N, 84°59′45″W, *Grijalva 396* (CM, HNMN, MO); "Kurinwacito," 80–100 m, 13°08′N, 84°55′W, *Moreno 23753* (MO); 2 km N of Kuikainita, S of Siuna, 100 m, *Neill 4150* (MO); Cerro Livico, 7 km NE of Siuna, 500 m, *Neill 3630* (MO); ca. 13 km above Kururia, road to San Jerónimo, <200 m, *Pipoly 3831* (MO); Cerro Baká, ca. 6.5 km E of Río Coperna, 200–300 m, 13°40′N, 84°30′W, *Pipoly 4918* (MO); Cerro La Pimienta number 1, ca. 900–980 m, ca. 13°45′N, 84°59′W, *Pipoly 5118* (MO); ca. 6.3 km S of Colonia Yolaina, ca. 200–300 m, 11°36–37′N, 84°22′W, *Stevens 6419* (MO); along Caño Majagua, ca. 750–850 m, ca. 13°45′N, 85°00–01′W, *Stevens 6881* (BM, LL, MO); Cerro Saslaya–San José del Hormiguero, ca. 200–400 m, 13°44–45′N, 84°57–58′W, *Stevens 7076* (MO); road to Mina Nueva América, ca. 14.3 km N of El Empalme, *Stevens 8435* (MO); Colonia San José–Tomás Mejía Caño, ca. 40–150 m, ca. 11°53–54′N, 84°20′W, *Stevens 9011* (BM, MO); Bonanza–Constancia, 160–360 m, ca. 13°58′–14°01′N, 84°37–40′W, *Stevens 12466* (MO); ca. 1.5 km NE of Las Esperanza de Las Quebradas, 300–350 m, ca. 13°38′N, 85°02′W, *Stevens & Moreno 19353* (MO); Río Mico, El Recreo, ca. 30 m, *Standley 19749* (F). PANAMA. **Bocas del Toro**: Campamento Changuinola 1, 20 m, *Correa et al. 4067* (MO, PMA). **Coclé**: La Pintada–Coclecito, 5.3 mi. N of Llano Grande, 513 m, *Croat 49240* (MO); 5.6 mi. N of Llano Grande, 1.4 mi. N of Continental Divide, 150 m, 8°46′N, 80°27′W, *Croat 67478* (CM, L, MEXU, MO, PMA); El Valle de Anton, behind Club Campestre, *Croat 14278* (MO). **Darién**: Parque Nacional Cerro Pirre, Alturas de Nique region, near Cana Mine, 500 m, 7°45′N, 77°40′W, *McPherson 11584* (MO); Cerro Pirre region, Cana, 480 m, *Croat 38009* (MO, RSA); 550–760 m, 7°57′N, 77°46′W, *68871* (MO); *68954* (CAS, MO, NY); *Folsom 4417* (MO, PMA); near station along Río Perisenico, 110 m, 8°01′N, 77°44′W, *Croat & Zhu 77107* (MO); Río Paracida, 0–80 m, 8°N, 77°48′W, *Croat 68998* (MO); ca. 13 km E of Pucuro, 450–600 m, 8°03′N, 77°20′W, *Hammel et al. 16195* (MO, US). **Panamá**: El Llano–Cartí, 6.8 mi. N, 350 m, *Croat 49111* (MO).

Philodendron thalassicum Croat & Grayum, sp. nov. TYPE: Panama. Chiriquí: Fortuna Dam area, trail to meteorological station of Río Hornito, ca. 0.5 km S of Centro de Científicos, 1010–1030 m, 8°45′N, 82°18′W, 23 June 1994, *Croat & Zhu 76297* (holotype, MO–4619518–22; isotypes, AAU, B, CAS, CM, COL, CR, DUKE, EAP, F, GB, GH, HUA, IBE, K, LE, M, MEXU, NY, P, PMA, QCA, RSA, S, SCZ, SEL, TEX, U, US, VEN). Figures 408–410, 415.

Planta terrestris aut hemiepiphytica; internodia brevia longa, 2–4 cm diam.; cataphylla 14–46 cm longa, acute 2-costata, persistentia ut fibra; petiolus D-formatus, 38–109 cm longus, 2–14 mm diam., plerumque longior quam laminae; lamina triangulari-sagittata vel ovata, 42–77 cm longa, 16–52 cm lata, atriviridis supra, saepe veneta infra; inflorescentia 1–3; pedunculus 3–14 cm longus, 2–9 mm diam.; spatha 11–20 cm longa; lamina spathae extus alba vel creamea, intus viridalba; tubo spathae 3–7 cm longo, extus pallide viridi, intus virello vel albo; pistilla (4)5–7(8)-locularia; loculi 16–22-ovulati.

Terrestrial or hemiepiphytic, growing to 4 m high in trees; stem appressed-climbing; internodes short, 2–4 cm diam., dark green, semiglossy, drying light yellowish brown, epidermis fragmented, reddish brown; roots several per node, <30 cm long, drying dark brown with epidermis ridged and splitting; cataphylls soft, 14–46 cm long, sharply 2-ribbed (ribs low), green or tinged pink when young to reddish brown or brown, drying brownish, persisting semi-intact, soon dilacerating; **petioles** 38–109 cm long, 2–14 mm diam., D-shaped, firm, flexible, sometimes with low, medial rib adaxially and with adaxial margins obtuse to rounded, medium green, weakly glossy, faintly to conspicuously dark- or striate-lineate, drying yellow-brown, dark brown to sometimes blackened; **blades** triangular-sagittate to ovate-triangular, subcoriaceous, conspicuously bicolorous, acuminate to long-acuminate at apex, sagittate at base, 42–77 cm long, 16–52 cm wide (0.8–1.8 times longer than wide), (0.6–1.4 times longer than petiole), usually shorter than petiole (averaging 0.9 times as long), upper surface dark green, matte or weakly glossy, sometimes glistening, drying dark brown, lower surface much paler (forming an areolate pattern on high magnification) and matte, often bluish green to whitish, drying bluish green if triangular-sagittate or yellowish brown if ovate-triangular, glaucous; anterior lobe 28–58 cm long, 18–51 cm wide (1.6–3.3 times longer than posterior lobes); posterior lobes broadly obtuse to narrowly rounded, 13.5–25 cm long, 10–23 cm wide, rounded; sinus spathulate to parabolic, 9–12 cm deep; midrib broadly sunken to flat above, slightly paler, obtusely triangular and darker below;

basal veins 5–11 per side, with 1–2(3) free to base, with a few veins coalesced for 5–9 cm; posterior rib prominently naked to 2.5–5 cm; primary lateral veins (4)12–18 per side, departing midrib at a 50–60° angle, weakly arcuate to ± straight to the margins, C-shaped to sunken and slightly paler above, convex and concolorous below; minor veins conspicuous, darker than surface to obscure below, arising from both the midrib and primary lateral veins. INFLORESCENCES ± erect, 1–3 per axil; peduncle 3–14 cm long, 2–9 mm diam., coarsely white-striate; **spathe** 11–20 cm long (1.15–2.8(4.7) times longer than peduncle); spathe blade white to cream and densely short-lineate outside, greenish white inside; spathe tube pale green and short-lineate outside, 3–7 cm long, greenish to white, sometimes faintly pinkish inside; **spadix** sessile to weakly stipitate; 12.8–16.6 cm long; pistillate portion 5.5 cm long in front, 3–3.5 cm long in back, 1.6–2 cm diam. midway, 1.5–1.6 cm diam. ca. 1 cm from apex; staminate portion 6.8–9.4 cm long; fertile staminate portion tapered toward apex, constricted (to 8–10 mm, 1.5–2 cm above base of sterile section) above sterile male flowers, 1 cm diam. at base, 1–1.6 cm diam. at middle, 5–7 mm diam. near apex; sterile staminate portion 1–1.7 cm diam. at base, 1 cm diam. at apex; pistils 2.8–3.8(6.2) mm long, 1.2 mm diam.; ovary (4)5–7(8)-locular, 1.7–2.3 mm diam., with axile placentation, wall sometimes embedded with angular crystal-like particles; locules 2.7(4.9) mm long, 0.5–0.6 mm diam.; ovules ca. 16–22 per locule, 2-seriate, 0.2–0.4 mm long, longer than funicle; funicle 0.1–0.2 mm long, adnate to lower part of partition; stigma lobed; style 1.3–2.1 mm diam., similar to style type B; style apex sloping to somewhat rounded, drying granular with an acute, turned up margin; stylar pores thickened, usually fused with the crown, sometimes free or nearly so, each with its own fringe of stigmatic papillae; style boss broad, shallow to quite shallow; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 0.9–1.2 mm long; thecae oblong, ± parallel to one another; sterile staminate flowers prismatic to weakly clavate, irregularly 5–6-sided, 1.2–1.6 mm long. INFRUCTESCENCE with berries whitish (maturing).

Flowering in *Philodendron thalassicum* occurs throughout the dry season to the mid-rainy season (January through August), though no flowering collections are known from Feburary (although post-anthesis collections do exist). Post-anthesis collections are known from April and May, and especially June, July, and August, and also from November (indicating that flowering may occur later than August). Immature fruiting collections are known from January, February, June, September, and November.

Philodendron thalassicum ranges from central Costa Rica to western Panama (Chiriquí) at (775)1000 to 2100 m elevation in *Premontane rain forest, Tropical Lower Montane wet forest,* and *Tropical Lower Montane rain forest* life zones.

Philodendron thalassicum is a member of *P.* sect. *Philodendron* subsect. *Philodendron* ser. *Impolita.* This species is characterized by its short thick internodes, two-ribbed cataphylls persisting as fibers, more or less D-shaped petioles (averaging longer than the blades), internally greenish to white spathe tube, and especially by the pale matte, often bluish green lower leaf surfaces. The epithet "thalassicum" (from thalassicus, meaning sea green or bluish green) is derived from this coloration of the lower blade surface.

Philodendron thalassicum may be confused with *P. hebetatum* and *P. strictum,* which also have matte, much paler lower blade surfaces. Both differ in having subterete petioles drying conspicuously light yellow-brown, rather than sharply D-shaped and drying somewhat blackened as in *P. thalassicum.* In addition, both *P. hebetatum* and *P. strictum* have cataphylls drying yellowish and semi-intact and spathe tubes colored reddish, maroon, or violet-purple within.

Plants of *P. thalassicum* with sagittate blades might be confused with narrow-leaved plants of *P. jodavisianum* or *P. tenue,* but both of those species have blades that are semiglossy to glossy (not at all glaucous) below. More ovate blade-forms of *P. thalassicum* might be confused with *P. schottianum,* but the latter also usually has a semiglossy lower blade surface, cataphylls that persist semi-intact, and spathe tubes reddish internally.

Philodendron thalassicum is variable in blade shape, with some triangular-sagittate (e.g., *Grayum et al. 3760, Croat 15876, 15745*) and others ovate (e.g., *Burger & Burger 7541, Burger & Stolze 5661, Burger & Liesner 6745*). Those with ovate leaves sometimes dry brownish on the lower surface while those with the triangular-sagittate blades dry bluish green. No other differences between these two forms have been detected.

Additional specimens examined. COSTA RICA. **Alajuela**: Cantón Alfaro Ruiz, Tapesco de Zarcero, 1650 m, *A. Smith NY1232* (F, NY); Alto Palomo, 1900 m, *Lent 1844* (CR, F); Naranjo–Quesada, along Hwy. 15, 3.2 mi. N of Zapote, 1560 m, *Croat 46908* (MO); Cantón San Ramón, R. B. Monteverde, Cordillera de Tilarán, valle del Río Peñas Blancas, 1600 m, 10°19′15″N, 84°46′30″W, *Bello 5151* (CR, INB, MO, NY); Monteverde reserve, 10°20′N, 85°50′W, *Croat 61191* (cultivated) (MO). **Car-**

tago: Moravia, 3.5 km from Finca Racine, 1200–1300 m, *Croat 36634* (CR, MO); Moravia de Chirripó–Turrialba, 1400–1600 m, *I. Chacón 269* (MO); Río Dos Amigos–Río Villegas, W of Río Grande de Orosi, ca. 1650 m, 9°42′N, 83°47′W, *Grayum et al. 3760* (MO, RSA); Quebrada Honda–Río Sombrero, ca. 1–2 km above El Muñeco, ca. 1400 m, *Luteyn 3238* (DUKE); ca. 20 km E of Río Pacuare, on road toward Moravia, 1150 m, 9°50′N, 83°24′W, *Thompson & Rawlins 1234* (CM); Quebrada Cangreja, 3 km S of Pan-American Highway, 1620–1650 m, 9°46′N, 83°57′W, *Liesner & Judziewicz 14498* (CR, MO); Tapantí Hydroelectric Reserve, ca. 1 km S of junction of Quebrada Salto and Río Grande de Orosi, 1500–1800 m, 9°43′N, 83°47′W, *Croat 36211* (MO); 1500–1700 m, *36078* (MO); 1525–1595 m, *79049* (CR, INB, MO); *Croat & Grayum 68290* (MO, US); *Grayum & French 5821* (INB, MO); 1600 m, *Lent 964* (CR, F, US); 1500 m, 9°42′N, 83°47′W, *Burger & Liesner 6745* (F, US); 1600 m, 9°42′N, 83°47′W, *Burger & Stolze 5661* (CR, DS, F, WIS); 5,200 ft., *Utley & Utley 7284* (MO); 1400–1700 m, *5184* (DUKE, MO); ca. 1600 m, 9°42′N, 83°46′W, *Burger & Burger 7541* (F, MO); 1400–1600 m, 9°42′N, 83°47′W, *Baker & Utley 201* (F, MO); Río Navarro, El Muñeco, 1400–1500 m, *Standley & Torres 51371* (US). **Heredia**: 4 mi. N of Vara Blanca, 1350 m, *Croat 35595* (MO); *35621* (MO); 9 km SE of San Ramón [de Sarapiquí], 1000 m, 10°16′N, 84°05′W, *Loiselle 138* (MO); Paracito–Río Claro, vic. of Bajo La Hondura, 1100–1400 m, *Croat 44500* (MO); Parque Nacional Braulio Carrillo, San Rafael de Vara Blanca, 1830 m, 10°11′50″N, 84°06′35″W, *Herrera 246* (MO); Sarapiquí, 1750 m, 10°12′47″N, 84°06′05″W, *Boyle & Boyle 2695* (MO); Finca Montreal, between headwaters of Río Volcán and Río San Fernando, 1800 m, 10°12′39″N, 84°06′45″W, *Boyle 1084* (CR, MO); Volcán Barva, Río Peje–Río Sardinal, Atlantic slope, 1200–1400 m, 10°15′30″N, 84°05′W, *Grayum & Herrera 7846* (MO); Río San Rafael, 1500 m, 10°13′N, 84°05′W, *Grayum 7050* (MO). **Limón**: Cordillera de Talamanca, Kamuk massif, 1900–2300 m, 9°14–15′N, 82°59′W, *Davidse & Herrera 29201* (MO). **Puntarenas**: Las Cruces Tropical Botanical Garden, 6 km W of San Vito de Java, 1200 m, 8°49′N, 82°58′W, *Croat 57264* (CR, MO); Río Coto Brus, near Cotón, 23 km N of La Unión (on Panama border), *Croat 26685* (CR, MO); Cerro Frantzius–Cerro Pittier, around Río Canasta, 9.5 airline km NW of Agua Caliente, 1500–1600 m, 9°02′N, 82°59′W, *Davidse et al. 28365* (CR, MO, NY); Quebrada Kuisa, near crossing of Ujarrás–San José Cabécar trail, 2100 m, 9°20′30″N, 83°14′W, *Grayum 10282* (CR, INB, MO); Monteverde Reserve, 1500 m, 10°17′N, 84°48′W, *Hammel et al. 14206* (MO); 1500–1600 m, 10°18′N, 84°47′W, *Haber & Zuchowski 10020* (CR, INB, MO, MV); 1500–1620 m, *Pounds 334* (CM, MO); *357* (MO); 1450–1650 m, *Burger & Baker 9772* (F, MO); Cerros Centinelas, 1550–1600 m, 10°18′N, 84°47′W, *Grayum & Sleeper 3857* (CR, MO). **San José**: trail beyond Bajo La Hondura, towards Río Claro, 1100–1200 m, *Luteyn 3318* (DUKE, MO); NE slope of Altos Tablazo, between Quebrada Tablazo and summit of ridge, 1700–1875 m, 9°50′N, 84°02′W, *Grayum & Schatz 5181* (CR, MO); Parque Nacional Braulio Carrillo, Estación La Montura, *Gómez et al. 20827* (CR, MO); General Valley, 1500 m, 9°27′N, 83°43′W, *Burger & Barringer 11601* (F, MO); Cerro Hondura, between Río Patria and Río Zurquí, 1500–1600 m, 10°04′N, 84°01′W, *Grayum & Sleeper 6131* (CM, MO). PANAMA. **Chiriquí**: NW side of Cerro Pando, *Croat 15966* (MO); Fortuna Lake area, along Continental Divide, 1200 m, 8°44′N, 81°17′W, *Croat 74975* (L, MO, NY, PMA, QCA); Río Hornito–Río Chiriquí, 1050–1100 m, ca. 8°44′N, 82°13′W, *Stevens 18371* (MO); Boquete region, Monte Rey, *Croat 15876* (MO), *15745* (MO); SW slope of Cerro Pate Macho, 1630–1780 m, 8°46′N, 82°25′W, *Croat 66401* (CAS, F, K, MBM, MO, TEX, W); Quiel road, 10 km above Boquete, 5500 ft., *Proctor 31831* (LL); Río Palo Alto–Cerro Pate Macho, ca. 6 km NE of Boquete, 1600–1700 m, 8°48′N, 82°23.5′W, *Grayum et al. 6359* (MO, PMA, US); Cerro Horqueta, ca. 1650 m, *Croat 27000A* (MO).

Philodendron tripartitum (Jacq.) Schott, Wiener Z. Kunst 1829: 780. 1829. *Arum tripartitum* Jacq., Pl. hort. schoenbr. 2: 33, t. 190. 1797. *Caladium tripartitum* (Jacq.) Willd., Sp. pl. 4: 491. 1805. TYPE: t. 190 in Jacq., Pl. hort. schoenbr. 1797 (holotype). Figures 411, 412, 416–424.

Philodendron fenzlii Engl., in Mart., Fl. Bras. 3(2): 144. 1878. TYPE: Mexico (holotype, B? lost). Schott ic. 2599 (neotype, here designated, W).

Philodendron affine Hemsl., Diagn. Pl. Nov. Mexic. 37. 1879. TYPE: Guatemala. Barranca Honda, Volcán de Fuego, *Salvin s.n.* (holotype, K).

Philodendron tripartitum var. *tricuspidatum* Engl., in Mart., Fl. Bras. 3(2): 144. 1878. TYPE: Costa Rica. San José: 1300 m, May 1857, *C. Hoffmann s.n.* (B? not seen).

Hemiepiphytic; appressed-climbing, stem often several meters long, sap watery, very aromatic-scented; internodes moderately elongate except near the apex, semiglossy, drying coarsely and irregularly ribbed (the ribs usually acute), 3–14 cm long, 1–2 cm diam. (to 3.5 cm diam. in Colombia), green to dark green to gray-green, soon drying light brown, epidermis sometimes loose and papery, roots usually 3–6 per node, usually less than 20 cm long, drying brown, less than 3 mm diam., semiglossy, sparsely scaly; cataphylls thin, (10)18–33 cm long, usually unribbed, sometimes sharply 1-ribbed, greenish, sometimes tinged reddish, deciduous intact. LEAVES erect-spreading to spreading; **petioles** 20–61 cm long, 6–15 mm diam., terete to subterete, moderately spongy, sometimes obtusely somewhat flattened, sometimes with an obtuse medial rib, dark green, surface glossy to weakly glossy; **blades** deeply 3-lobed almost to the base or rarely trisect, ca. as broad as long in outline, thinly coriaceous, semiglossy, moderately bicolorous, acuminate at apex, lower surface sometimes heavily tinged purplish or reddish; typically rather dissimilar, median segment usually oblanceolate, sometimes nearly elliptic, rarely oblong to linear, 15–45 cm long, (4.5)7–14(19) cm wide, 1.9–7.8 times longer than wide (averaging 4.3 times longer than wide), ((0.9)1.5(1.7) times longer than lateral segments); the lateral segments conspicuously ine-

quilateral, arcuate-spreading toward apex, (12)18–35 cm long, 1.3–15 cm wide, the inner margin always much narrower than the outer margin and weakly confluent with medial lobe, usually to 1 cm, rarely to 2 cm, the outer margin 1.5–5 times wider than the inner margin where the difference is most severe; midrib broadly convex, concolorous above, convex to round-raised, darker below; basal veins lacking; primary lateral veins (4)6–10(12) per side, departing midrib to a 25° angle on narrow blades or to 90° angle on broader blades, weakly curved on narrow blades or markedly curved on broader blades to the margins, sunken and usually concolorous above, convex and darker than surface below; minor veins fine and conspicuously visible, arising from both the midrib and primary lateral veins. INFLORESCENCES usually solitary, sometimes 2–3 per axil; peduncle 3–16 cm long, 6–13 cm diam., medium green, moderately recurved with reddish ring around the apex; **spathe** (8)13–21 cm long, 1.2–4 cm diam., weakly constricted above the tube, to 2.5 cm diam. at constriction, usually medium green to yellow-green, rarely creamy white, with dark purple dots (most to 3 mm circumference) heavily so on tube, less so on blade throughout, white to creamy white or greenish white within, cucullate at apex, convolute in lower ⅔ of tube at base, margins whitish or colorless, recurled at anthesis; spathe blade glossy, smooth outside, (the opening 7.5–8.5 cm long, 3.4–5.2 cm wide), creamy white, glossy; resin canals intermittent, orange, appearing medially and extending into spathe tube inside; spathe tube oblong, glossy outside, 5 cm long, 3 cm diam., maroon, deep red, or purplish-violet inside; **spadix** sessile or shortly stipitate (to 2 mm); clavate, ± erect, 12.3 cm long, broadest above the middle, weakly constricted between sterile and fertile portions; pistillate portion greenish white to pale yellowish green, 2.5–4.5(6.2) cm long, 1–1.8 cm diam. throughout; staminate portion 7.5–8.5 cm long; fertile staminate portion creamy white, 1.2 cm diam. at base, 1.3 cm diam. at middle, 1 cm diam. ca. 1 cm from apex, broadest in the middle, usually narrower than the pistillate and sterile portions; sterile staminate portion usually broader than the pistillate portion, creamy white, drying yellowish, 1.3 mm diam.; pistils 1.7–2.5(3.4) mm long, 0.6–1.1(2.3) mm diam.; ovary 6–8(10)-locular, 0.8–2.3 mm long, 1.1–2.3 mm diam., with sub-basal placentation; locules 0.8–1.1(2.3) mm long, 0.2–0.4(0.7) mm diam.; ovule sac 0.7–0.9(1.2) mm long; ovules 1–2 per locule, contained within a translucent and gelatinous matrix, 0.4–0.6 mm long, longer than funicle; funicle 0.2–0.4 mm long (can be pulled free to base), style 0.4–0.8 mm long, 1–1.4(2.5) mm diam., usually similar to style type D (rarely B or E); style apex ± rounded; stigma subdiscoid, truncate, 0.7 mm diam., 0.2–0.3 mm high, covering center of style apex, inserted on style boss; the androecium truncate, prismatic, margins usually irregularly 5-sided, 1.4 mm long, 2.2 mm diam. at apex; thecae oblong, 0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, prismatic, irregularly 4–6-sided, 1.9 mm long, 1.5–2 mm wide. Berries whitish, irregularly angular, 4 mm long, 2–2.7 mm diam.; seeds usually 6–8 per berry, cylindrical, 1.5 mm long, sticky. JUVENILE plants with blades maroon below.

Flowering in *Philodendron tripartitum* occurs throughout the dry season and the first half of the rainy season (mostly May through July), with seemingly little phenological variation throughout its range. Most flowering collections have been made from January through July with a few from August and also November. Post-anthesis inflorescences have been collected throughout the whole year with the greatest concentration from May to July. Immature fruits are known from January, April, July, August, September, and November, while mature fruits are known only from October.

Philodendron tripartitum ranges from Mexico to Ecuador from near sea level to 1300(1500) m elevation. In Central America, this species ranges along the Caribbean slope in Mexico (Veracruz to Tabasco) and throughout Middle America, but occurs on both slopes in Costa Rica and Panama thence along the Pacific slope into lowland Antioquia and Chocó Departments, Colombia. In Mexico, *Philodendron tripartitum* occurs in Selva Alta Perennifolia and the transition forest to Bosque Caducifolia. In Costa Rica and Panama, it occurs in *Tropical moist forest* to *Premontane wet forest, Tropical wet forest,* and *Premontane rain forest.* In Colombia, it is known from *Tropical wet forest* and *Tropical rain forest.*

Philodendron tripartitum is a member of *P.* sect. *Tritomophyllum.* This species is characterized by its elongate internodes, deeply trilobate leaf blades only weakly confluent at the base or sometimes completely trisect, and spathes scarcely constricted above the tube.

Philodendron tripartitum is most likely confused with the common *P. anisotomum.* See under the latter species for the differences. It is probably most closely related to *P. cotobrusense* from Costa Rica, which differs in having elliptic medial lobes with 18 or more pairs of primary lateral veins. *Philodendron tripartitum* may be confused also with *P.*

madronoense from Panama. That species also differs in having elliptic medial lobes with about 25 pair of primary lateral veins.

Along with *P. sagittifolium*, *P. tripartitum* is one of the most highly variable and widespread species in the genus, with complex patterns of variation in the shape of the lobes, the degree to which the lobes are confluent, the number of primary lateral veins, and the size and number of inflorescences per axil. Clinal variations range both north and south throughout Mexico and Central America and also elevationally. Most Mexican specimens have the lobes conspicuously confluent at the base with the lateral lobes moderately to prominently auriculate, and all have one inflorescence per axil. This form is well characterized by Engler's drawings of Araceae Drawing no. 48 of the synonym, *P. fenzlii*. In Mexico, *P. tripartitum* ranges from sea level to usually about 900 m elevation.

To the south and east in Central America, especially at lower elevations, the blades of *P. tripartitum* dry paler green and are more weakly confluent at the base or completely trisect with the lateral lobes only weakly auriculate. This form is encountered in eastern Chiapas and Tabasco and ranges through Belize and the remainder of Caribbean coastal Central America, as well as on the Pacific coast of El Salvador. It reaches its most deeply trisect and pale green expression in *Tropical Moist forest* along the Caribbean coast of Panama, but also at lower elevations along the Pacific slope in Darién Province. In contrast to material from Mexico and Belize, this form of the species generally has but a single inflorescence per axil, though in Panama it may have from one to three inflorescences per axil. Noteworthy collections of this form are *Dressler 1513* and *Breedlove 10330* from eastern Chiapas, which have blades drying pale yellow-green and weakly confluent with only weakly auriculate lateral lobes, yet occur at between 950 and 1266 m (3800 ft.) elevation.

Most collections of *P. tripartitum* from above 500 m and from wet life zones (e.g., *Premontane wet forest* and *Tropical wet forest*) in Nicaragua, Costa Rica, and western Panama (Chiriquí Province) have typically dark-drying blades with moderately confluent and auriculate lateral lobes. Collections from the highlands of Nicaragua and Costa Rica may have one to three inflorescences per axil, and each inflorescence is typically smaller than when but a single inflorescence is present.

Collections from lowland southwestern Costa Rica on the Pacific Coast differ from those of lowland Pacific coastal Panama and El Salvador in having the lobes more broadly confluent; more prominently auriculate lateral lobes; broader medial lobes, with more numerous primary lateral veins; and in often drying more yellowish brown. Particularly noteworthy is *Davidse 24202* from the Costa Rican highlands southeast of Las Alturas. It has comparably broadly convolute lateral lobes and approaches *P. cotobrusense* in having medial lobes with closer, more numerous primary lateral veins and five inflorescences per axil. It is conceivably a hybrid with that species.

Collections from central Panama, especially El Valle and the vicinity of Cerro Jefe, exhibit extreme variation in leaf morphology and even spathe coloration. This is true to a lesser extent elsewhere in Panama, at Santa Fe, along the El Llano–Cartí Road, and on the Santa Rita Ridge Road. In Coclé, typical plants have somewhat blackened leaf blades with slender, weakly auriculate and weakly confluent lobes. These collections have the medial lobe ranging from 4.4 to 7.2 times longer than wide. This same narrow-lobed variation occurs also on Cerro Jefe and the Santa Rita Ridge Road where the lobes may be proportionately even more slender, ranging from 7.3 to 13 times longer than wide. Two collections from the El Llano–Cartí Road, *Thompson 4704* and *Miller et al. 862*, have somewhat larger blades with the medial lobes five to six times longer than wide. These narrow-leaved forms vary from having 1–2 relatively large inflorescences per axil (*Luteyn 4066*) or with up to three smaller inflorescences per axil (*Gentry 7433*). The spathes are variously reported as reddish green or red-brown, to pink, red, or purple.

Spathe color is not variable throughout most of Central America, where the spathe tube is generally green outside but maroon in the lower two-thirds within. Spathe color becomes more variable in Panama, where in the narrow-lobed forms (mentioned above) it may be reported as purplish or red. As one approaches South America, spathe color becomes more variable. In eastern Panama at the Serranía de Majé and in Darién Province, the spathe is reported as green mottled purple (*Whitefoord & Eddy 223*) or yellow-green with purple flecks (*Churchill & de Nevers 4480*), or even cream with red spots (*Knapp & Mallet 3160*). There seems to be no correlation with either elevation or the degree to which the lobes are confluent or auriculate.

Style type in *P. tripartitum* is also variable. Throughout most of its range, from Mexico to Panama along the Caribbean coast, the style is raised and button-shaped (Mayo style type D). Generally, the stylar canals emerge onto the surface near the outer margin of the style through moderately large pores on a generally flattened apex. However, some

collections, notably *Grayum et al. 5034* from 600 m in Heredia Province in Costa Rica, have pores somewhat pie-shaped and the general level of the apex somewhat sunken. More extreme manifestations of this phenomenon are present in *Grayum 6979* (studied in reconstituted condition), from Heredia Province at 700–900 m and *Croat & Porter 16241*, from Bocas del Toro Province, Panama, near sea level. In these collections the style type might more appropriately be referred to as a Mayo style type E since it is definitely funnel-shaped with a distinct marginal rim. In *Grayum 6979* the style is broadly bowl-shaped with moderately large pores situated about midway between the annulus and the center. In *Croat & Porter 16241* the funnel is held above the surface of the style in dried condition, with the margins curled under, and there are radial ribs on the inside of the funnel just as there are in the *Grayum et al. 5034* collection. It is also similar to the latter collection and the remainder of the type D styles in having large pores positioned along the outer edge of the nearly straight-walled funnel. Indicating that these style types are probably merely variations of the D-type style is the fact that *Gómez et al. 21988* from the highlands of Puntarenas Province has both extremes of style types represented on both of the above-mentioned collections.

Three other style types are also present in *P. tripartitum* and may ultimately allow separation of distinct subspecies because they occur in more isolated populations. One of these is Mayo style type E, represented by specimens collected from the Pacific slope of Costa Rica, e.g., *Croat 35248* from San Isidro–Dominical Road at 1000 m, and *Burger & Stolze 5473* from Rincón de Osa. In this type of style the stylar pores are smaller than in type D and are arranged in a smaller circle at the base of the funnel. Similar to the material from southwestern Costa Rica in this respect is a collection from Darién Province, Panama, near the Colombian border (*Whitefoord & Eddy 223*).

The second novel type of style is present on collections from higher elevations in Panama, e.g., *Croat 66228* from Chiriquí Province and *Croat 69721* from Darién Province. This style type is perhaps sufficiently different to warrant the recognition of these collections as a distinct subspecies. It is similar to Mayo style type B, except that the style is weakly sunken rather than flattened. The stigmatic papillae may cover the entire concave area or they may arise primarily from the center. The stylar pores are smaller than in style type D, and are arranged in a tight circle at the center of the funnel, much as in the case of style type E in southwestern Costa Rica. In this case, however, there is no sign of a protruded funnel, so apparent on collections from the latter area.

While the style types mentioned here seem to warrant recognition of two or more subspecies in *P. tripartitum*, the highly variable general morphology of the species and the general state of preservation of the ovaries of most collections precludes the thorough analysis needed.

Standley and Steyermark (1958a) reported the fruits of *P. tripartitum* as red, but this is unsubstantiated. Bunting (1965) stated that the locules are strictly 1-ovulate, whereas Standley and Steyermark (1958a) described them as 1–3-ovulate. Bunting's findings have here been confirmed.

Many of the variations discussed above, if considered in isolation, are distinctive and would appear to be worthy of recognition. However, considering the immense variation within populations, the overlapping characteristics, and the generally similar structure of the flowers, it seems best to consider this group a single but highly variable species.

This species was reported in Jacquin's (1797) original description for Venezuela, but it does not occur there. Since the type illustration (t. 190) clearly represents this species it must be presumed that Jacquin, who apparently described the plant from a cultivated collection, must have been confused about the origin of the material. Schott (1829), who transferred *Arum tripartitum* to *Philodendron*, claimed to have seen only living material, perhaps the same collection seen by Jacquin at Schönbrunn. Bunting (1979) excluded *P. tripartitum* from his treatment of the Araceae for Venezuela and used the name *P. holtonianum* Schott for a Venezuelan species with three-lobed species. The Jacquin plate (t. 190) clearly does not match *P. holtonianum*, which differs in having the lateral lobes more broadly confluent and not at all auriculate at the base with the posterior rib naked 3 to 5 cm at the base. In contrast, leaves of *P. tripartitum* are often noticeably auriculate with the posterior rib not at all naked. Krause (1913) treated *P. holtonianum* as a variety of *P. tripartitum* but these species, while superficially similar in blade shape, are probably not closely related.

Caladium trifoliatum Desf. was questionably included by Krause as a synonym of this species, but the description is of a plant with the lateral lobes petiolulate, whereas leaf blades in *P. tripartitum* are at most trisect, with the lateral lobes sessile.

Additional specimens examined. BELIZE. **Cayo**: *Lundell 6336* (CM, MICH); McCaw River–Cuevas, vic. of Milonario, 1900 ft., *Croat 23670* (MO). **Stann Creek**: Mid-

dlesex, *Gentle 2936* (CM, MICH). **Toledo**: Edwards Road beyond Columbia, *Gentle 6217* (LL); Jacinto Creek, *Gentle 6002* (LL); Monkey River, Monkey River–Cockscomb, *Gentle 4458* (LL, MICH); Punta Gorda, 1 mi. E of junction with road to San Antonio, 100 ft., *Croat 24509* (MO); SW Maya Mountains, Columbia River Forest Reserve, trail between Union and Gloria Camps, 700–750 m, 16°23′22″N, 89°08′10″W, *Holst 4388* (MO); Southern Maya Mountains, Bladen Nature Reserve, 260 m, 16°30′15″N, 88°55′07″W, *Davidse 35794* (BRH, MO). COSTA RICA. **Alajuela**: 22 km NE of Quesada by air, 4 km W of Muelle San Carlos, 10°28′N, 84°30′W, *Liesner 14121* (B, CR, MO); Río Peñas Blancas, below Monteverde Cloud Forest Nature Reserve, 1250–1350 m, 9°17′N, 84°86′W, *Burger et al. 10770* (CHAPA, NY); 850 m, *Bello 362* (CR, MO); 700–900 m, *Haber & Zuchowski 9468* (CR, MO); San Ramon, 820 m, 10°19′N, 84°43′W, *Bello & Eyol 2684* (INB, MO); 840 m, *Bello et al. 10870* (CR, INB); 15 km N of Boca Arenal, ca. 100 m, 10°38′N, 84°31′W, *Liesner et al. 15043* (CR, MO); Cañas–Upala, 13.8 km N of Bijagua, 100–150 m, *Croat 36447* (MO); 4 km NNE of Bijagua, ca. 400 m, *36253* (MO); Upala, 550 m, *Garcia 187* (CR, INB); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, *Croat 43593* (MO). **Cartago**: Turrialba, *Cook & Doyle 378* (US); Moravia–Quebrada Platanillo (Tsipirí), ca. 1250 m, *Croat 36659* (MO); 4 km SE of Pejibaye along Río Gato, 700 m, 9°48′N, 83°42′W, *Liesner 14342* (CR, MO). **Guanacaste**: Volcán Miravalles, ca. 800 m, 10°42′N, 85°07′W, *Burger & Gentry 9127* (CR, F, U); Parque Nacional Rincón de la Vieja, Volcán Santa María, 900–1200 m, 10°47′N 85°18′W, *Davidse et al. 23313* (CR, MO); 840 m, *Rivera 479* (CR, MO). **Heredia**: La Selva Field Station, 100 m, *Grayum 3019* (DUKE); *3033* (DUKE); *2444* (DUKE); 100 m, *2863* (DUKE); *Croat 44227* (MO); *Grayum & Sperry 2212* (DUKE); *Sperry 982* (DUKE); *Folsom 10011* (DUKE); Quebrada Tigre–Río Sardinal, ca. 9 km SW of Las Horquetas, ca. 600 m, 10°17′N, 84°02′W, *Grayum et al. 5034* (MO); Volcán Barva, 700–950 m, 10°17′30″N, 84°04′30″W, *Grayum 6979* (MBM, MO, W); Route 9, 3 km S of La Virgen de Sarapiquí, 200 m, *Woodruff 188* (FLAS); 9 km SE of San Ramón, 1000 m, 10°16′N, 84°05′W, *Loiselle 161* (MO); San Ramón, *Tonduz 17719A* (K, P). **Limón**: ca. 4–5 airline km S of Islas Buena Vista in the Río Colorado, 100–180 m, 10°38′40″N, 83°41′W, *Davidse & Herrera 31293* (CR, MO); Hitoy Cerere reserve, SW of Valle La Estrella, 150–550 m, 9°39′N, 83°02′W, *Grayum et al. 5809* (MO); 2 km W of Río Toro Amarillo, W of Guápiles, 275 m, 10°13′N, 83°50′W, *Thompson & Rawlins 1217* (CM); Hone Creek–Cahuita, *Gómez et al. 20523* (MO); ca. 1 km N of Shiroles, ca. 50 m, *Croat 43277* (MO); ca. 10 mi. S of Punta Cahuita, ca. 3 mi. S of turnoff to Bribrí, ca. 70 m, *Croat 43202* (MO); vic. Laguna Pereira, 2–4 m, 10°47–49′N, 83°37′W, *Stevens et al. 25184* (MO); Guápiles, 850 ft., *J. D. Smith 4981* (US); 30 m, *Robles 2241* (CR, MO); Los Angeles, San Miguel, 1100 m, 10°06′40″N, 83°59′40″W, *Herrera & Schik 3826* (CR, INB, MO); Parque Nacional Tortuguero, 40 m, 10°28′N, 83°34′W, *Robles 1738* (CR, MO). **Puntarenas**: Cordillera de Talamanca, 2160 m, 9°20′20″N, 83°13′55″W, *Bittner 1787* (INB, MO); Parque Nacional Corcovado Estación Sirena, sea level, 8°28′N, 83°35′W, *Knapp 2189* (F, MO, NY, US); 1–50 m, *Kernan & Phillips 1090* (CR, MO); 220 m, 8°34′N, 83°31′W, *Aguilar 2848* (CR, INB); Rincón de Osa, 20–150 m, *Liesner 1991* (MO, US); Fila El Tigre, SE of Las Alturas, 1350–1450 m, 8°56′N, 82°51′W, *Davidse 24202* (B, MO); Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 1500–1600 m, 9°02′N, 82°59′W, *Davidse et al. 28422* (CR, MO); Osa Península, Rancho Quemado, ca. 15 km W of Rincón, 200 m, 8°40′N, 83°34′W, *Hammel et al. 16981* (CR, MO); Chacarita–Rincón de Osa, 10 km W of Chacarita, ca. 100 m, 8°45′N, 83°18′W, *Croat & Grayum 59881* (MO); Osa, Agua Buena, 60–70 m, 8°41′32″N, 83°30′21″W, *Ramírez 223* (CR, MO); vic. Rincón de Osa, 50–200 m, 8°42′N, 83°31′W, *Burger & Gentry 8922* (F); 20–60 m, *Utley & Utley 1234* (F, MO); 30 m, 8°42′N, 83°31′W, *Burger & Stolze 5473* (CR, F, US); Quebrada Vaquedano, 500 m, 8°38′45″N, 83°35′25″W, *Herrera 4013* (CR, MO); La Tigra–Las Mellizas, 1280 m, *Gómez et al. 21988* (MO); Palmar Norte, trail to Jalisco, 50–700 m, *Croat 35193* (MO); 6 km S of San Vito de Java, ca. 5000 ft., *Raven 21852* (CR, DH, DS); Río Bella Vista near Las Alturas, 1300 m, 8°56′N, 82°51′W, *Lent 2686* (CR, F); Finca Las Alturas, at Cotón, Río Cotón, ca. 1300 m, *Croat 44362* (MO); La Unión–Cotón, Río Negro–Río Coto Brus, *Croat 26582* (MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1150 m, *Croat 22295* (MO); Burica Peninsula, Quebrada Palito, 20–270 m, *Croat 22617* (MO). **San José**: El General Valley, vic. of San Isidro El General, 730 m, *Molina et al. 18308* (EAP, F, NY, US); San Isidro del General–Dominical, above Alfombra, 1000 m, 9°18′N, 83°46′W, *Burger & Baker 10113* (F); 990–1100 m, *Croat & Hannon 79108* (INB, MO); 2 km N of Dominical along CR-223, 40–100 m, *Utley & Utley 4944* (DUKE); ca. 4.5 mi. SW of Canaán road from Rivas, ca. 900 m, *Croat 43438* (MO), *43446* (MO); 9 mi. SW of Río Pacuar, 680 m, *Croat 35342* (MO); SW of San Isidro, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35248* (MO). EL SALVADOR. Jardín Botánico, Zona 23SC, 800 m, 13°40′N, 89°15′W, *Villacorta 317* (LAGU, MO). GUATEMALA. **Alta Verapaz**: near Finca Sepacuite, *Cook & Griggs 743* (US); Chamá, *Johnson 404* (CM, US); Cubilqüitz, 350 m, *Tuerckheim 8023* (US); *J. D. Smith 8023* (US); Pantín, below Tamahú, 600 m, *Standley 70543* (F); 4 mi. up road to Oxec, N off Highway 7E, ca. 6 km NE of Panzós, 500 m, *Croat 41610* (MO); 9 mi. up road to Oxec, 800 m, *41684* (MO). **Izabal**: near Entre Ríos, 18 m, *Standley 72745* (F). **Petén**: Dolores, km 83, Machaquila Road, *Contreras 2115* (LL). HONDURAS. **Atlántida**: Lancetilla Reserve, near Tela, 70–150 m, 15°44′N, 87°27′W, *Croat 42670* (MO); *Croat & Hannon 64640* (MO, NY); *Standley 53381* (F, US); S of San Alejo near Río San Alejo, 150–270 m, *Standley 7962* (F); ca. 10 km SW of La Ceiba, 80–150 m, 15°42′N, 86°51′W, *Liesner 26077* (MO). **Gracias a Díos**: Ahuas Bila, 200 km SW of Puerto Lempira, 100 m, *Nelson & Cruz 9181* (MO, UNAH); Río Plátano, 84°40–85′N, 15°30–55′W, *Clewell & Cruz 4062* (CHAPA, MO, UC). **Morazán**: vic. El Zamorano, 800 m, *Molina 34354* (MO). **Yoro**: Texíguat River, 1 km SW of San José de Texíguat, 100–400 m, 15°30′N, 87°26′W, *Hazlett & Brant 8047* (MO); Río Guán Guán, ca. 3 km S of San José de Texíguat, 380 m, 15°30′N, 87°27′W, *Evans 1323* (MO). MEXICO. **Chiapas**: 27–43 km SW of Palenque, 210–810 m, *Croat 40335* (MO), *40306* (MO); 460 m, *Croat 40269* (MO); 20 mi. N of Ocozocoautla, 700 m, *Croat 40634* (MO, NY); 13 mi. N of Ocozocoautla, 900 m, *Croat 40620* (MO, NY); Mpio. Cintalapa, Oaxaca–Chiapas border, 4 km W of La Ciénega, 38 km W of Las Cruces, 1400 m, *Breedlove 25132* (MO); 5 km W of Bonampak, 350 m, *Martínez 6972* (MO); 2 km NE of Bonampak above Cojolite, 350 m, *7939* (MO); Laguna Ocotal Grande, 45 km E of Ocosingo, *Dressler 1513* (GH, US); 10 mi. N of Ocozocoautla, 3800 ft., *Breedlove 10330* (F); km 18 on road to Malpasco (N of Ocozo-

cautla), 2700 ft., *Kennedy 1426* (SEL); Bochil–Pichucalco, 17.1 km SW of Pichucalco, 430 m, *Croat 78662* (CHIP, MO). **Oaxaca**: Uxpanapa region, 17 km E of Sarabia, 100 m, 17°10′N, 94°45′W, *Croat & Hannon 63212* (B, BM, K, MO, NY, US); 150 m, 17°33′N, 92°59′W, *65367* (MO); Tuxtepec–Oaxaca, 6 mi. W of Valle Nacional on Highway 175, 660 m, *Croat 39741* (MO); 8 km SW of Valle Nacional, 400 m, *Hernández & Chacón 491* (INB, MO). **Tabasco**: Grutas de Ocona near Teapa, 20–100 m, *Davidse et al. 29509* (CM, MO); Teapa, cultivated, *Croat 59160* (MO); Mpio. Tacotalpa, 0.2 km NW of Tapijulapa, *Cowan et al. 3496* (CSAT, MO). **Veracruz**: Valle de Córdova, *Bourgeau s.n.* (P); Route 185, 4 km NE of Minatitlan, 50 m, *King 1113* (MICH): 6 mi. E of Coatzacoalcos, 10 m, *Croat 40058* (MO); 7 km NE of Sontecomapan, 0–50 m, 18°33′30″N, 94°59′W, *Nee 22607* (F, MO); 5 km NW of Pajapan, Cerro San Martín, 750–900 m, 18°17′20″N, 94°43′W, *Nee & Calzada 22697* (F, MO, NY); Los Tuxtlas, 200 m, 18°42′N, 95°10′W, *Croat 63163* (MICH, MO, US). NICARAGUA. 40–45 km SW of Waspam, 10–100 ft., *Seymour 3776* (MO). **Jinotega**: Río Bocay, Salto Acatulu, ca. 130 m, 14°13′N, 85°10′W, *Stevens et al. 16750* (MO). **Matagalpa**: Comarca Wanawás, Río Bilampí, 180–200 m, 12°03–02′N, 85°13′W, *Araquistain & Moreno 2401* (MO, SAR); Cerro Musún, path to Palán, 300–600 m, *Araquistain & Moreno 2471* (AAU, LE, MO); 20 km E of Matagalpa, along Río Yasica, 700 m, *Neill 1963* (MO); Cerro Musún, 500–800 m, *Araquistain & Moreno 2571* (MO); Cerro Musún, 8 km from village of Wanawás, 500–800 m, 12°59–13°N, 85°14′W, *Araquistain & Moreno 2359* (MO); Quebrada Negra, Rio Bilampí, 500 m, *Neill 1816* (MO, US). **Río San Juan**: Bocas de Sábalo, 70–100 m, 11°03′N, 84°27′W, *Moreno 26748* (MO); above Río Sábalo, 40 m, 11°03′N, 84°28′W, *Moreno & Robleto 26016* (MO). **Zelaya**: ca. 14.3 km N of El Empalme, *Stevens 8303* (BM, MO); El Empalme–Rosita, along new road to Mina Nueva América, *Stevens 12667* (MO); *12668* (MO); *Pipoly 5293* (MO); 15 km W of Rama, 100 ft., *Harmon & Fuentes 5079* (MO); Kuikuinita, S of Siuna, 160 m, *Neill 4132* (MO); Río Prinzapolka–Quebrada San Rafael, Waní, ca. 100 m, 13°42′N, 84°50′W, *Pipoly 4578* (MO); *4587* (MO); *4588* (MO); *4589* (MO); Waní–Siuna, near Río Matías, ca. 0–100 m, 13°43′N, 84°49′W, *Pipoly 4682* (MO); *4701* (MO); Colonia Yolania–Colonia Manantiales (Colonia Somoza), ca. 200–300 m, ca. 11°36–37′N, 84°22′W, *Stevens 4825* (MO); Rosita–Puerto Cabezas, ca. 15.7 km SW of Río Kukalaya, <100 m, 13°58′N, 84°12′W, *Stevens 8502* (MO); Caño Zamora on Río Rama, ca. 10 m, ca. 11°57′N, 84°16′W, *Stevens 8821* (MO); Bonanza–Constancia, 160–360 m, ca. 13°58′–14°01′N, 84°37–40′W, *Stevens 12482* (MO); *12455* (MO); El Empalme–Limbaika, ca. 3.9 km SE, ca. 65 m, 13°39′N, 84°24′W, *Stevens 12883* (MO); *12886* (MO); vic. of Bonanza, 200–350 m, 14°01′N, 84°35′W, *Stevens 13031* (MO); *13053* (MO); 250–350 m, ca. 14°02′N, 84°34–35′W, *18786* (MO); 7.4 m SE, ca. 130 m, 13°38′N, 84°23′W, *21752* (MEXU, MO); *12346* (MO); ca. 140 m, ca. 14°01′N, 84°34′W, *Stevens 8056* (BM, MO); 1 km N of "Las Mercedes" settlement, 160–180 m, *Vincelli 334A* (MO); "Bodega" region, 30 km NE of Río Blanco, 80–100 m, 13°03′N, 84°58′W, *Moreno 24078* (MO); "San Agustín," SE of Rama, ca. 60 m, 12°09′N, 84°12′W, *Robleto 564* (MO); *Neill 3632* (MO); Bonanza–El Salto Grande, Laguna Santa Rosita, ca. 140–160 m, 14°03′N, 84°37′W, *Pipoly 3687* (MO); Mpio. Siuna, La Pimienta, *Ortiz 1966* (MO); Río Mico, Experimental Station El Recreo, 30 m, 12°10′N, 84°18′W, *Davidse et al. 30768* (MO); Río Prinzapolka, ca. 2 km S of Waní, ca. 0–100 m, 13°42′N, 84°50′W, *Pipoly 4733* (MO), *4738* (MO), *4747* (MO); Río Punta Gorda, Atlanta, 10 m, 11°34′N, 84°01′W, *Moreno & Sandino 12769* (MO); Waspam–Puerto Cabezas, Río Troncera, <200 m, ca. 14°43′N, 84°06′W, *Pipoly 4042* (MO); Río Wilike Grande, Wilike region, 100 m, 13°05′N, 84°57′W, *Moreno 23999* (MO). PANAMA. **Bocas del Toro**: Fortuna Dam–Chiriquí Grande, 3.2 mi. N of Continental Divide, 700 m, 8°45′N, 82°15′W, *Croat & Grayum 60281* (MO); Changuinola–Almirante, Milla 7.5, *Croat & Porter 16241* (MO); Valle del Silencio, Río Changuinola, ca. 1 km above mouth of Río Teribe, <100 m, 9°21′40″N, 82°31′40″W, *Croat & Zhu 76431* (MO). **Canal Area**: Frijoles, 25–30 m, *Pittier 3755* (US); Barro Colorado Island, *Shattuck 182* (F, GH, MO); *Ebinger 99* (MO); *Croat 11838* (MO); *Schmalzel 797* (MO); *Dwyer et al. 8474* (MO); *Croat 16535* (MO); *15067* (MO); *11006* (MO); *10741* (MO, UC); *10198* (MO, SCZ); *10085* (MO); *6214* (MO); *6294* (MO); *8605* (MO); *8040* (MO); *6861* (MO); *6495* (MO); *4001* (MO); Summit Garden, *Croat 17058* (MO); *10284* (MO, SCZ); *33015* (MO); *10915* (MO). **Chiriquí**: Volcán–Serrano, 7 mi. N of Volcán, 8°50′N, 82°38′W, *Croat 66228* (MO); vic. El Hato del Volcán at Las Lagunas, 3 mi. from Nueva California, 1380 m, 8°46′N, 82°40′W, *Croat 67707* (MO, PMA); vic. Santa Clara, 1520 m, *Croat 66288* (F, MO); Gualaca–Chiriquí Grande 2.5 mi. beyond Los Planes de Hornito, 1099 m, 8°40′N, 82°13′W, *Croat 67739* (CM, MO); 2.8 mi. beyond Los Planes, 1200 m, *48817* (MO); Quebrada La Mina, 2.3 mi. N of Los Planes, 800 m, 8°41′N, 82°13′W, *Croat & Zhu 76364* (CM, MO); along Río Colorado, 1200–1400 m, 82°43′W, 8°50′N, *Hamilton & Krager 3757* (MO, RSA); vic. Boquete, ca. 1450 m, *Croat 26744* (MO). **Coclé**: La Mesa, N of El Valle de Antón, 800–900 m, 8°38′N, 80°09′W, *Croat 67210* (CM, MO); *Croat 13358* (MO); ca. 1 mi. N of El Valle, *Gentry & Dwyer 3591* (MO); 900 m, *Gentry 7433* (F, GH, MO). **Coclé–Panamá**: trail beyond La Mesa towards Los Llano and the border, *Luteyn 3178* (MO); 850–900 m, *Luteyn 4066* (MO). **Colón**: Santa Rita Ridge, 26 km from Transisthmian Highway, 500 m, 9°26′N, 79°57′W, *Knapp et al. 1708* (MO); Mile ca. 12, ca. 500 m, 9°25′N, 79°40′W, *McPherson 11760* (MO). **Darién**: Parque Nacional del Darién, ca. 17 km E of Pucuro, Río Pucuro, 750–850 m, 8°03.5′N, 77°17′W, *Hammel et al. 16293* (MO); western slopes of Cerro Pirre, 17 km N of El Real, Río Perisenico, 100 m, 8°01′N, 77°40W, *Croat & Zhu 77187* (MO); vic. Cana, 500–600 m, *Croat 37641* (MO); Alturas de Nique region, 900–1250 m, 7°45′N, 77°40′W, *McPherson 11603* (MO); Cerro Sapo, 800 ft., *Hammel 1330* (MO); E base of Cerro Sapo along stream (Río Celorio?), 1300 ft., *1131* (MO); 18 km SE of Jaque, 25 m, *Garwood et al. 98* (BM, CM, MO, PMA); N of Punta Guayabo Grande, NW of Ensenada El Guayabo ridges, 0–200 m, 7°24′N, 78°07′W, *Knapp & Mallet 3160* (MO, US); Río Coasi, Cerro Coasi, *Duke 15554* (US); Río Cocalito, SE of Jacque, 7°18′N, 77°58′W, *Whitefoord & Eddy 223* (BM, MEXU, MO). **Panamá**: Juan Díaz, *Standley 30618* (US); Cerro Jefe region, 750–800 m, 9°14′N, 79°22′W, *Croat 67082* (F, MO); *67084* (MO); 4.6 km beyond peak on road to Altos de Pacora, ca. 600 m, *Croat 35900* (MO); at Altos de Pacora, 750 m, 9°15′N, 79°29′W, *Croat & Zhu 76606* (MO); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68636* (CM, MO); Campo Tres, 5 km NE of Altos de Pacora, *Busey 835* (MO); Lago Cerro Azul, 500 m, *Sullivan 82* (MO); Cerro Campana, 2500 ft., *Hammel 3767* (MO, SEL); Río Majé–Quebrada Brava, 60 m, *Croat 34630* (MO); El Llano–Cartí Road, 7–12 km from

Interamerican Highway, 360–400 m, *Croat 25122* (MO); Km ca. 16–18, 400 m, *Tyson & Nee 7355* (MO); El Llano Cartí road, Mile 10.6, ca. 400 m, 9°17′N, 78°58′W, *Miller et al. 862* (MO); Mile 6–10, 200–250 m, 9°15–16′N, 78°59′W, *Thompson 4704* (CM, MO); Serranía de Majé, along Río Ipetí, near confluence with Río Ambrosio, 100 m, 8°57′N, 79°32′W, *Churchill & de Nevers 4480* (MO, PMA, RSA). **San Blas**: Nusagandi, along El Llano–Carti Road, 11.6 mi. N of highway, 450 m, 9°18′N, 79°59′W, *Croat 75135* (CM, MO, PMA). **Veraguas**: Santa Fe–Río San Luis, vic. Río Tercero Brazo, 700 m, 8°33′N, 81°08′W, *Croat 66925* (MO, PMA); Río Dos Bocas, ca. 5–8 km N of Alto Piedra, 730–770 m, *Croat 25915* (MO); ca. 500 m, *Croat 34242* (MO); vic. Escuela Agrícola–Calovébora, ca. 1200 m, 81°07′W, 8°32′N, *Hamilton et al. 1279* (MO).

Philodendron tysonii Croat, sp. nov. TYPE: Panama. Chiriquí: Gualaca–Chiriquí Grande, 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *Croat 67844* (holotype, MO–3614677; isotypes, AAU, B, CAS, CM, CR, DUKE, F, GH, K, M, MEXU, NY, P, PMA, RSA, US, VEN, W). Figures 29, 425–430.

Planta plerumque hemiepiphytica, interdum terrestris; internodia 2–6 cm longa, 3.5–4 cm diam.; cataphylla (10)21–33 cm longa, incostata vel leniter 1-costata, saepe rubella, persistentia semi-intacta, demum decidua; petiolus teres vel subteres, 39–90 cm longus, 8–15 mm diam.; lamina ovata, coriacea, nitida, 32–70 cm longa, 24–50 cm lata; costa postica plerumque vix aut haud nuda, raro nuda 3 cm; inflorescentia 4–5; pedunculus 3–12 cm longus, 3–8(11) mm diam.; spatha 11.5–19 cm longa, lamina spathae extus viridi, suffusa marronina aut rubella, intus alba vel pallide viridi; tubo spathae extus suffuso marronino aut rubello, intus atrimarronina suffuso in laminam; pistilla (5)6–8(9)-locularia; loculi (4)5–7-ovulati.

Usually hemiepiphytic, appressed-climber, sometimes terrestrial; internodes short, stout, semiglossy, smooth, 2–6 cm long, 3.5–4 cm diam., dark green; roots elongate, fine, branched; cataphylls (10)21–33 cm long, unribbed to weakly 1-ribbed, sometimes sharply 2-ribbed near base and unribbed near apex, frequently reddish, frequently striate, emarginate at apex, persisting semi-intact at upper nodes, eventually deciduous, emarginate at apex; **petioles** 39–90 cm long, 8–15 mm diam., terete to subterete, surface densely pale-striate, glossy; sheath 10.5–11 cm long; **blades** ovate, coriaceous to moderately coriaceous, glossy to semiglossy, conspicuously bicolorous, acuminate at apex (the acumen sometimes inrolled and twisted), cordate at base, 32–70 cm long, 24–50 cm wide (1–1.8 times longer than wide and averaging 1.4 times), (0.4–1.1 times longer than petiole), averaging about ¾ as long as petiole, upper surface dark green, drying dark brown to blackish brown, lower surface slightly paler, drying dark yellow-brown to greenish brown; anterior lobe 25–52.5 cm long, 20–50 cm wide (2–4.8 times longer than than posterior lobes); posterior lobes broadly rounded to broadly obtuse, 8–20 cm long, 11–22 cm wide; sinus parabolic, sometimes spatulate, (3)4–12 cm deep; midrib broadly convex to almost flat, conspicuously paler than surface above, convex to bluntly acute, darker than surface below; basal veins 5–9 per side, with (0)1(2) free to base, numbers 3–4 coalesced 1.5–3 cm; posterior rib usually scarcely or not at all naked, rarely naked for 3 cm; primary lateral veins 4–10 per side, departing midrib at a 60–70° angle, moderately straight to the margins, narrowly sunken above, convex and somewhat paler than surface below; interprimary veins sunken, usually concolorous above, raised, darker than surface below; minor veins moderately distinct below, arising from both the midrib and primary lateral veins. INFLORESCENCES 4–5 per axil; peduncle 3–12 cm long, 3–8(11) mm diam., green, finely striate; **spathe** 11.5–19 cm long (1.5–4.5 times longer than peduncle); spathe blade green to white, lightly to heavily tinged maroon or reddish, finely striate-speckled, margins clear outside, white to pale green inside; spathe tube tinged maroon or reddish, finely striate-speckled outside, 4.5–10 cm long, dark maroon, suffused into blade inside, weakly constricted above the tube; **spadix** white throughout, 10.7–15.6 cm long; pistillate portion 3.4–5.2 cm long in front, 2.4–3.1 cm long in back, broadest midway and gradually tapered toward both ends, 1.2 cm diam. at apex, 1.2–1.4 cm diam. at middle; staminate portion 7.7–9.4 cm long; fertile staminate portion white, barely constricted above the sterile staminate portion, barely tapered toward apex, 1–1.2 cm diam. at base, 1–1.2 cm diam. at middle, 6–7 mm diam. ca. 1 cm from apex; sterile staminate portion 9–10 mm diam.; pistils 1.5–2.7 mm long, 0.8–1.6 mm diam., white; ovary (5)6–8(9)-locular, with sub-basal placentation; locules (0.8)1.1–1.3 mm long, 0.3–0.6 mm diam.; ovules (4)5–7 per locule, (0.1)0.3–0.4 mm long, 2-seriate, contained within transparent ovule sac; style similar to style type B; stigma 0.8–1.2 mm diam., 0.2–0.3 mm high. INFRUCTESCENCE with pistillate spadix 6.5 cm long, 4 cm diam.

Flowering in *Philodendron tysonii* occurs mostly in June and July but also in September. In reality, flowering probably occurs from January through September or perhaps October, since post-anthesis collections have been made nearly throughout the year except February. Immature fruiting collections have been made in March, September, and November.

Philodendron tysonii is known only from Panama, but is expected to be found in the Cordillera

de Talamanca of Costa Rica. It ranges from 600 to 1500 m elevation in *Premontane rain forest* and *Tropical Lower Montane rain forest* life zones.

Philodendron tysonii is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Reticulata*. This species is characterized by its stout, short (usually 3–5 cm diam.) internodes; unribbed or weakly one-ribbed, frequently reddish cataphylls persisting semi-intact (often becoming fibrous) at the upper nodes; terete to subterete petioles; and ovate-cordate blades averaging 1.4 times longer than wide and about three-fourths as long as the petioles, with 6–9 basal veins and a weakly developed posterior rib, which is rarely naked at the sinus.

Philodendron tysonii is perhaps most easily confused with *P. antonioanum*, with which it may occur. The latter species differs in having sharply 2-ribbed cataphylls, blades drying gray-green with prominulous "cross-veins" and 4 to 6 pairs of primary lateral veins, and short-pedunculate inflorescences with spathe tubes dark magenta on both surfaces and barely constricted above. In contrast, *P. tysonii* has usually bluntly 1-ribbed cataphylls, blades drying ± blackened and smooth above, 6–10 primary lateral veins, more prominently pedunculate inflorescences, and prominently constricted spathes merely tinged red on the tube outside. In addition, the two species differ in the nature of their ovules, with *P. tysonii* having (5)6–8(9)-locular ovaries with (4)5–7 ovules per locule borne in an envelope with sub-basal placentation, while *P. antonioanum* has 5-locular ovaries with about 30 ovules per locule, with parietal placentation and not borne in an envelope.

This species may also be confused with *P. sagittifolium* (especially broader-leaved forms), which shares blades with mostly free basal veins with posterior ribs short or lacking and scarcely or not at all naked along the sinus. The latter species differs in having narrower stems (rarely more than 3 cm diam.), green, sharply 2-ribbed deciduous cataphylls (vs. persistent in *P. tysonii*), and blades usually somewhat reddish brown and proportionately longer (averaging about 2 times longer than broad) with the posterior lobes usually narrowly rounded. In addition, the juvenile blades of *P. sagittifolium* are elongated, usually oblong to narrowly triangular, and usually up to 2.5 times longer than wide (vs. ovate to narrowly ovate, less than 2.5 times longer than wide, and with broadly rounded posterior lobes in *P. tysonii*).

Additional specimens examined. PANAMA. **Bocas del Toro**: Fortuna Dam area, Gualaca–Chiriquí Grande, just N of the Continental Divide, 850–950 m, 8°46′N, 82°17′W, *Hammel et al. 14700* (MO); ca. 8.5 mi. from bridge over Fortuna Lake, 600 m, 8°46′N, 82°16′W, *Croat 67005* (CAS, CM, L, MO, PMA, TEX); Cerro Colorado, 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69017* (DUKE, IBE, MEXU, MO, NY, PMA, QCA, RSA, WIS); 7 mi. from Chame, ca. 1500 m, 8°35′N, 81°45′W, *McPherson 8810* (MO); 5.3 mi. N of center of Fortuna Dam, Continental Divide Trail, 8°44′N, 82°17′W, *Croat & Zhu 76346* (MO); near Lago Fortuna, along trail to Río Hornito, 8°45′N, 82°18′W, *Croat & Zhu 76374* (MO, PMA). **Chiriquí**: Cerro Colorado, above San Félix, 18–27 mi. N of Pan-American Highway, 1200–1500 m, *Croat 33148* (MO); 24 mi. N of Río San Félix, 1430–1500 m, *48486* (MO); 34.1 km N of Río San Félix, 1390 m, *37258* (MO); 28 mi. above Río San Félix, 1200–1500 m, *33269* (MO); from Chame to ca. 9 mi. along road, 1100–1750 m, 8°35′N, 81°54′W, *Hammel & Trainer 15008* (MO, NY); Fortuna Dam area, Fortuna–Chiriquí Grande, Continental Divide, 1170 m, 8°44′N, 81°17′W, *Croat 66711* (B, BR, COL, CR, K, MO, NY, PMA, US); *Hammel & Kress 13490* (DUKE); Continental Divide trail, 8°44′N, 82°17′W, *Croat & Zhu 76330* (K, MO, NY, SCZ, US); trail to Río Hornito, 1100–1350 m, 8°45′N, 82°15′W, *McPherson 11660* (MO); *Croat & Zhu 76417* (AAU, CM, ENCB, GB, IBE, M, MO, NY, PMA, TEX, WIS); confluence of Río Hornito and Río Chiriquí, 1050–1100 m, ca. 8°44′N, 82°13′W, *Stevens 18376* (MO); *18377* (MO); vic. IRHE facilities, 1100–1200 m, 8°45′N, 82°08′W, *Croat 66589* (AAU, COL, DUKE, F, K, MBM, MEXU, MO, P, PMA, US, VDB); 1300 m, *Croat 48760* (CM, MO); Quebrada Los Chorros–Quebrada Frank, N of reservoir, 1100 m, 8°45′N, 82°13′W, *Churchill & Churchill 6081* (MO); 8.3 mi. beyond Los Planes de Hornito, 1260 m, 8°44′N, 82°16′W, *Croat 49943* (MO); 1300 m, 8°45′N, 82°17′W, *49821* (MO); 1400 m, *48704* (AAU, MEXU, MO, U, UC, W). **Coclé**: El Copé region, Alto Calvario, Continental Divide, 9.4 km above El Copé, 750–900 m, *Croat 44719* (MO); 710–800 m, 8°39′N, 80°36′W, *68766* (MO, PMA); 850 m, *67577* (AAU, CM, F, G, L, MEXU, MO, NY, PMA, TEX, US); 930 m, *49203* (MO); 650–850 m, *Folsom 6217* (MO). **Panamá**: Cerro Jefe region, vic. of summit, 9°15′N, 79°30′W, *Croat & Zhu 76210* (CM, MO); *Witherspoon & Witherspoon 8531* (MO); ca. 1000 m, *Croat 49084* (CAS, K, MO, PMA); 1000 m, 9°15′N, 79°30′W, *Knapp 2240* (MO); La Eneida, 1000 m, *Luteyn & Kennedy 1775* (DUKE); 0.8 mi. beyond turnoff to Altos de Pacora, 770 m, 9°15′N, 79°29′W, *Croat & Zhu 76614* (CM, MO, WIS); 3–3.5 mi. NE of Altos de Pacora, 700–750 m, 9°15′N, 79°25′W, *Croat 68688* (AAU, CM, F, G, MEXU, MO, PMA, TEX, US); 800–1000 m, *22671* (F, MO); 2400 ft., *Antonio 4753* (MO); *Croat 67059* (AAU, B, BR, C, CAS, CM, COL, CR, DUKE, EAP, ENCB, F, HNMN, HUA, IBE, JAUM, JBGP, K, L, M, MO, NY, PMA, QCA, US, USCG, WIS); 850–900 m, 9°15′N, 79°30′W, *McDonagh et al. 36* (BM); ca. 1000 m, *Mori et al. 3737* (MO); ca. 950 m, ca. 9°15′N, 79°30′W, *McPherson 7109* (MO); Cerro Azul–Cerro Jefe, ca. 1000 m, *Luteyn 3209* (DUKE); 3000 ft., *Tyson et al. 4449A* (MO, SCZ); Campo Tres, ca. 700 m, *Croat 27047* (F, L, MO, US); El Llano–Cartí, 6.8 mi. from highway, 350 m, *Croat 49120* (MO). **Veraguas**: Santa Fe region, Alto Piedra–Calorébora, 3200–5600 ft., *Hammel 4604* (MO); Río Tercero Brazo, beyond Alto Piedra, *Croat 27328* (MO); between Río Tercero Brazo and summit of hill leading down to the Atlantic lowlands, 700 m, 8°33′N, 81°08′W, *Croat 66926* (B, CAS, F, K, MO, PMA, US); Parque Nacional Cerro Tute, near Alto Piedra,

0.5 mi. N of Alto Piedra, 1250–1350 m, *Croat 48955* (F, MO); 800–1030 m, *Croat & Zhu 76911* (CM, MO).

Philodendron ubigantupense Croat, sp. nov. TYPE: Panama. San Blas: on mainland opposite Isla Miria Ubigantupo, along trail to Digole, to 20 m, 9°26′N, 78°54′W, 19 July 1987, *H. Herrera 294* (holotype, MO–3585503; isotype, PMA). Figure 436.

Planta hemiepiphytica; internodia usque to 7.5 cm longa, 1 cm diam.; cataphylla decidua; petiolus subteres, 12–13 cm longus, in sicco 5–6 mm diam.; lamina oblonga, anguste cordulata basi, 27–32 cm longa, 8.5–9 cm lata, in sicco caniviridis; nervis lateralibus 1 obscuris; inflorescentia 1; pedunculus 8 cm longus, in sicco 5 mm diam.; spatha 9.3 cm longa, viridis; pistilla (7)8-locularia; loculi 1-ovulati.

Hemiepiphytic; stem scandent; internodes to 7.5 cm long, 1 cm diam., slender, drying 7 mm diam., gray-brown, irregularly and closely fissured, somewhat flaking; roots several per node, drying moderately smooth, reddish brown, semiglossy; cataphylls lanceolate, deciduous; **petioles** 12–13 cm long, drying 5–6 mm diam., subterete, drying dark gray-brown, minutely striate, sheathed to 1.5 cm; **blades** oblong, acuminate at apex (the acumen tightly inrolled, 5 mm long), narrowly cordulate at base, 27–32 cm long, 8.5–9 cm wide (3–3.8 times longer than wide), (2.2–2.5 times longer than petiole), about as long as petiole; upper surface dark green, drying weakly glossy, gray-green, lower surface slightly paler, semiglossy, drying greenish gray; sinus to 1.3 cm deep; midrib broadly convex above, convex and paler below, drying faintly striate; primary lateral veins almost totally obscure above and below; many minor veins, all free to base, arising from the midrib only, drying obscure above, close and weakly raised below, spreading at a 55–75° angle, ± straight to the margin. INFLORESCENCES solitary; peduncle 8 cm long, drying 5 mm diam.; **spathe** green, 9.3 cm long, (1.2 times longer than peduncle); spathe tube weakly constricted, ca. 4.5 cm long; **spadix** bluntly pointed at apex, 10.8 cm long; pistillate portion 4 cm long in front, 3.7 cm long in back, 8 mm diam. at apex, drying 1 cm diam. at middle; staminate portion 8.1 cm long; fertile staminate portion 8.5 mm diam. at middle, 6.5 mm diam. ca. 1 cm from apex; sterile staminate portion 8 mm diam. at apex, 9 mm diam. at base; pistils 1.5 mm long; ovary (7)8-locular, 1.2 mm diam., with sub-basal placentation; locules 1.1 mm long, 0.2–0.3 mm diam.; ovule sac ca. 1 mm long; ovules 1 per locule, contained within transparent ovule sac, ca. 0.3 mm long; funicle ca. 0.3 mm long (can be pulled free to base), style 0.9 mm diam., similar to style type D; style apex sloping to weakly rounded; style boss moderately broad and fairly pronounced; the androecium truncate, sometimes prismatic and weakly clavate, margins irregularly 4–5-sided, 0.8–1.5 mm long; thecae oblong, 0.2–0.3 mm wide, ± parallel to one another; sterile staminate flowers clavate to prismatic, irregularly 4–5-sided, 1.3–1.7 mm long.

The flowering phenology of *Philodendron ubigantupense* is uncertain owing to its rarity, but since it has small inflorescences and was in flower in July, it probably both flowers and fruits in the wet season.

Philodendron ubigantupense is endemic to Panama, known only from the type locality along the Atlantic coast, at or near sea level in a *Premontane wet forest* life zone.

Philodendron ubigantupense is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is characterized by its scandent habit, long, slender internodes, subterete petioles and especially by its oblong, gray-green drying blades over twice as long as the petioles, weakly cordulate leaf bases, and almost totally obscure primary lateral veins.

Philodendron ubigantupense is perhaps most similar to *P. folsomii,* which has blades of similar size and color. The latter species differs in having short internodes and blades merely rounded at the base and with 8–10 distinct primary lateral veins. In addition, *P. folsomii* has 6–7 locules per ovary, whereas *P. ubigantupense* has mostly 8 locules per ovary. *Philodendron immixtum* is another species that might be confused with *P. ubigantupense,* but it differs in having proportionately broader blades (to 2.8 times longer than broad) with up to five, obvious primary lateral veins.

Philodendron utleyanum, Croat, sp. nov. TYPE: Panama. Colón: Santa Rita Ridge, about 7 mi. from Transisthmian Highway, ca. 200 m, 21 Dec. 1971, *Wilbur et al. 15068* (holotype, DUKE 226389). Figures 431, 432.

Planta hemiepiphytica; internodia 1–3.5 cm longa, 1.5–2 cm diam., in sicco pallide brunnea; cataphylla usque 27 cm longa, leniter 2-costata, in sicco obscure rubribrunnea, decidua; petiolus subteres, atribrunneus, obtuse subcomplanatus adaxialiter versus apicem, 19–21.5 cm longus, in sicco 6–7 cm diam.; lamina oblongo-oblanceolata, 32–39 cm longa, 10–14 cm lata, aliquantum inequilaterala et rotundata vel truncata aut leniter cordulata basi, atriviridis supra, in sicco canobrunnea, saepe aliquantum rubella infra, in sicco brunnea; nervis basalibus 2–3 utroque, omnibus liberis ad basim; inflorescentia 1; pedunculus usque 9 cm longus, in sicco atribrunneus; spatha usque 11 cm longa, pallide viridis, extus suffusa

subrosea, intus alba, tubo spathae 5 cm longa; pistilla 4–5-locularia; loculi 1-ovulati.

Hemiepiphytic; stem appressed-climbing; internodes drying moderately glossy, irregularly and acutely ribbed with a few flat smooth intervening areas, 1–3.5 cm long, 1.5–2 cm diam., drying light brown; roots several per node, short, drying brown, to 3 cm diam.; cataphylls to 27 cm long, weakly 2-ribbed, but sharply 2-ribbed toward the apex, red tinged toward the base, drying dull reddish brown, deciduous; **petioles** 19–21.5 cm long, drying 6–7 cm diam., subterete, dark brown, obtusely somewhat flattened toward the apex adaxially, surface smooth to weakly ribbed; **blades** somewhat inequilateral, oblong-oblanceolate, subcoriaceous, semiglossy, acuminate at apex, somewhat inequilateral and rounded to truncate to weakly cordulate at base, 32–39 cm long, 10–14 cm wide, broadest above the middle, 1.3–1.8 times longer than petioles, upper surface dark green, drying gray-brown, lower surface often somewhat reddish, drying medium brown; posterior lobes to ca. 2 cm long; midrib drying weakly and obtusely raised, slightly paler than surface above, drying convex, drying light brown with a distinct pale border along its edges and paler than surface below; basal veins 2–3 per side, and with all free to base; primary lateral veins 8–9 per side, departing midrib at a 65–80° angle in the lower one-half, to 45° angle toward apex, weakly arcuate to the margins, drying inconspicuous except near the midrib, paler than surface above, weakly convex and paler than surface, sometimes undulate below; minor veins drying moderately inconspicuous and close, weakly undulate, arising from the midrib only, the surface and minor veins minutely and densely granular at 10× magnification. INFLORESCENCES 1 per axil; peduncle to 9 cm long, drying 4.5 mm diam., dark brown; **spathe** moderately coriaceous, to 11 cm long, ca. 2 cm diam., pale green with pinkish tinge, drying dark brown throughout, white within; spathe tube 5 cm long, 1.8–2 cm diam.; **spadix** sessile, 10 cm long.; pistillate portion 5 cm long, drying to 1.7 cm diam. near base, 1.5 cm diam. midway, 1 cm at apex; staminate portion 4.7 cm long, too deteriorated for detailed studies; pistils 2.5–3 mm long, 1.5–2 mm diam., drying light brown, smooth except warty near apex; style type not studied; stigma 0.4–0.6 m diam., button-like on drying with a medial nipple and 4–5 radiate arms, sometimes with fragments of the dried stigma apron-like still attached; locules 4–5; ovaries with sub-basal placentation, 1 ovule per locule.

Flowering in *Philodendron utleyanum* is poorly known. The single collection with immature fruits was made in December. This species probably flowers in the rainy season.

Philodendron utleyanum is endemic to Panama, known only by the type specimen from Colón Province in a region of *Premontane wet forest* at 200 m elevation.

Philodendron utleyanum is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is distinguished by its short tan internodes; sharply 2-ribbed, deciduous cataphylls; subterete petioles about three-fourths as long as the blades; and oblong-oblanceolate, brown-drying blades broadest above the middle and rounded to weakly subcordate at the base.

In terms of coloration and texture, *P. utleyanum* appears closest to *P. sagittifolium,* but in terms of blade shape it is closest to *P. pseudauriculatum.* The former differs in having the blades broadest at the base and decidedly cordate, the latter in having dark gray-green-drying leaves, more or less spongy, proportionately shorter petioles, and the spadix clearly demarcated from the peduncles by a marked color contrast. *Philodendron utleyanum* lacks any clear limit between the peduncle and the spathe.

This species is named in honor of John Utley, a participant in the Duke University expedition that collected the type. Utley has been responsible for collecting many interesting and important Araceae during his trips to Central America and during his tenure as a Peace Corps volunteer in Costa Rica.

Philodendron verapazense Croat, sp. nov. TYPE: Guatemala. Alta Verapaz: 7 mi. on road to Oxec, along road turning N off Hwy. 7E between Tucurú and El Estor, ca. 6 km NE of Panzós, 700 m, ca. 15°28′N, 89°04′W, *Croat 41656* (holotype, MO–2743518; isotypes, GUAT, US). Figures 433–435.

Planta hemiepiphytica; internodia longiora quam lata, conspicue multisulcata; cataphylla 14–17 cm longa, acute 2-costata, decidua; petiolus acute D-formatus complanatus adaxialiter, 29–44 longus, in sicco 2–5 mm diam.; lamina anguste ovato-triangulari-cordata, longe acuminata apice, longe cordata vel sagittata basi, 26–34 cm longa, 11.5–14 cm lata; nervis lateralibus I 3–4 utroque; inflorescentia 1; pedunculus 3–14 cm longus, 4–5 mm diam.; spatha 10–18 cm longa, extus rubriviolacea; tubo spathae intus carmesino; pistilla 4–6-loculari; loculi 2-ovulati.

Hemiepiphytic; stem appressed-climbing or sometimes scandent; pre-adult internodes to 20 cm long, 1.5–3 cm long; adult internodes green becoming tinged purple, finally tan, conspicuously many-sulcate except above each petiole, longer than broad; roots few per node, 10–30 cm long,

drying dark brown, weakly glossy, 2.3 mm diam.; cataphylls 14–17 cm long, sharply 2-ribbed, green tinged red, deciduous; **petioles** 29–44 cm long, drying 2–5 mm diam., sharply D-shaped, flattened adaxially, with adaxial margins sharp; **blades** narrowly ovate-triangular-cordate, subcoriaceous, long-acuminate at apex (the acumen sometimes apiculate), long-cordate to sagittate at base, 26–34 cm long, 11.5–14 cm wide (2–3 times longer than wide), (0.7–1.1 times longer than petiole); anterior lobe (13)21–26 cm long, (5.4)13–14 cm wide (2.9–4.3 times longer than posterior lobes); posterior lobes 6–7.5 cm long, (2.3)6–7.1 cm wide; sinus hippocrepiform, sometimes spathulate, 7–7.5 cm deep; midrib broadly convex and paler above, convex and darker below, drying somewhat acute; basal veins 3(4) per side, with 0(1) free to base, the remainder coalesced 2–2.5 cm; posterior rib naked for most or all of its length; primary lateral veins 3–4 per side, departing midrib at a 55–65° angle, ± straight to weakly arcuate to the margins; minor veins arising from the midrib only. INFLORESCENCES 1 per axil; peduncle 3–14 cm long, 4–5 mm diam., green or tinged with reddish violet; **spathe** 10–18 cm long ((0.7)2–3.7 times longer than peduncle), reddish violet outside; spathe blade acuminate; spathe tube cylindrical, 8–9 cm long, 1–1.5 cm diam., crimson-red inside; **spadix** stipitate to 3.5 cm long; acute at apex, 15–16.5 cm long, constricted ca. 4 cm above base of sterile staminate portion; pistillate portion cream, 3.2 cm long in front, 1.7 cm long in back, 1.5–2.6 cm wide at base; staminate portion 8.3–9 cm long; fertile staminate portion cream, tapered to apex, 7–10 mm diam. at base and midway, 3–4 mm diam. ca. 1 cm from apex; sterile staminate portion 1.8–2.2 mm diam.; pistils 1.9–2.3 mm long; ovary 4–6-locular, 1 mm diam., with sub-basal placentation; locules 0.9 mm long, ca. 0.3 mm diam.; ovule sac 0.4–1 mm long; ovules 2 per locule, contained within transparent, gelatinous ovule sac, longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.8 mm diam., similar to style type D; style apex somewhat rounded to flat, depressions surrounding stylar canal exits, style boss broad, very shallow; the androecium truncate, prismatic, ± oblong, margins irregularly 5–6-sided, 0.8–1.1 mm long; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another, very nearly contiguous; sterile staminate flowers prismatic to weakly clavate, irregularly 4–6-sided, mostly 5-sided, 1.3–1.9 mm long.

Flowering in *Philodendron verapazense* occurs in April and May, with a single, post-anthesis collection known from July.

Philodendron verapazense ranges from southern Mexico (Chiapas) to Guatemala (Alta Verapaz), at 700 to 1525 m elevation in "Bosque Pino-Encino" in Mexico and *Tropical moist forest* in Guatemala.

Philodendron verapazense is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is recognized by its scandent habit with the internodes longer than broad and conspicuously pluri-sulcate, as well as by its sharply two-ribbed, deciduous cataphylls, sharply D-shaped petioles, narrowly ovate-triangular-cordate blades, solitary inflorescences, red to reddish violet spathe tubes, and greenish spathe blades.

Philodendron verapazense is probably most similar to *P. sagittifolium* especially in the shape and coloration of the blades, the sharply two-ribbed, deciduous cataphylls, and the D-shaped petioles. It differs from the latter species principally in its deeply sulcate stems, sharply D-shaped, shorter (less than 50 cm long) petioles, and leaf blades with 3–4 pairs of primary lateral veins (vs. subterete, longer petioles, which are greater than 50 cm long, and 4–8 pairs of primary lateral veins for *P. sagittifolium*).

Additional specimens examined. GUATEMALA. **Alta Verapaz**: near Chirriacté, on the Petén Highway, ca. 900 m, *Standley 91978* (F). **Izabal**: vic. EXMIBAL camp 2, NW of Lake Izabal, 400–500 m, *Jones & Facey 3354* (NY). MEXICO. **Chiapas**: Los Lagos, 3 mi. NW of Rancho San José, 5000 ft., *Carlson 1846* (F).

Philodendron verrucosum L. Mathieu ex Schott, Syn. Aroid. 85. 1856. TYPE: Locality unknown (holotype, W? lost?). Schott ic. 2757–2759 (neotype, here designated). Figures 437–440, 445.

Philodendron daguense Linden & André, Ill. Hort. 18: 192, t. 79. 1871. TYPE: Colombia. Valle: Río Dagua, *Wallis s.n.* (holotype, K).

Philodendron pilatonense Engl., Bot. Jahrb. Syst. 37: 129. 1905. TYPE: Ecuador. Pichincha: Río Pilatón, May 1899, *Sodiro s.n.* (holotype, B; isotypes, G, MO).

Philodendron discolor K. Krause, Notizbl. Bot. Gard. Berlin-Dahlem 9: 273. 1925. TYPE: Peru. Junín: Prov. Jauja, in the valley of Río Masamerich (Río Pontachuela) confluent of Río Pangoa, above Rasthütte Calabaza, 1500–1600 m, 11°30′S, 7 May 1913, *Weberbauer 6663* (holotype, B; isotype, F).

Usually hemiepiphytic, rarely terrestrial or epiphytic; stem appressed-climbing, densely scaly or setose, trichomes green to greenish white; pre-adult internodes to 20 cm long, 1–2 cm diam.; adult internodes smooth, scurfy, minutely wrinkled, semiglossy to matte, 3–10 cm long, 2–6 cm diam., about as long as broad or longer than broad, gray to brown, roots moderately numerous, mostly short,

covered at least on one side with fine root hairs, drying dark brown, semiglossy, faintly appressed-scaly; cataphylls 10–30 cm long, unribbed, sometimes bluntly 1-ribbed, green or reddish, densely scaly or setose, persisting as a tangled network of fibers. LEAVES erect-spreading; **petioles** 33–65(90) cm long, 3 cm diam. at base, 1.5 cm diam. at apex, subterete, purplish violet to brownish, surface densely scaly, the scales of two distinct types, short, broad, often lacerate scales interspersed with long acicular scales, the latter erect, or spreading then erect; **blades** broadly ovate-cordate, thinly coriaceous, moderately bicolorous, acuminate to narrow acuminate at apex (the acumen mostly inrolled, 1–2.5 mm long), cordate at base, 28–75 cm long, 19–60 cm wide (1–1.7 times longer than wide), (0.7–1.5 times longer than petiole), broadest below point of petiole attachment, upper surface dark green or bronze-green (blackish green on new leaves), velvety to matte, drying dark brown, yellow-green or gray-green, lower surface pale green tinged red-purple between secondary veins (weakly glossy and purple-violet on new leaves), matte, drying yellow-brown to reddish brown; anterior lobe 9.6–51 cm long, 10–59 cm wide (1.9–3 times longer than posterior lobes); posterior lobes 8–21 cm long, 5–28 cm wide, broadly rounded to obtuse; sinus hippocrepiform to obovate or closed; midrib flat to sunken, slightly paler than surface above, convex, matte, darker than surface below; basal veins 6–8 per side, with (0)1–2 free to base, numbers 3–4 coalesced 1–5 cm; posterior rib not at all naked on small blades or naked for 0.5–6 cm; primary lateral veins 3–6(8) per side, departing midrib at a 50–55° angle, sunken, paler than surface above, round-raised to convex, darker than surface below; minor veins distinct and darker than surface below, arising from both the midrib and primary lateral veins; "cross-veins" conspicuous, in part raised below. INFLORESCENCES 1–4 per axil; peduncles 5–25 cm long, 1–2 cm diam., medium green to purplish, usually 0.66–1.75 times longer than the spathe; **spathe** densely scaly or setose, 10–22 cm long, 4 cm diam.; spathe blade medium green, whitish or reddish green outside, white to pinkish inside; spathe tube reddish green, medium green, or dull purple-violet outside, red or pale reddish (dark green post-anthesis) inside; **spadix** 14.6 cm long; pistillate portion cylindrical to weakly clavate, 1.8–4.6 cm long, 1 cm diam. at apex, 8 mm wide at base; staminate portion 9.4 cm long; fertile staminate portion cream; pistils 2.6–3.3 mm long, 1.4–1.7 mm diam.; ovary 4–5-locular, 1.9–2.5 mm long, 1.4–1.7 mm diam., with axile placentation; locules 1.9–2.5 mm long, 0.5–0.7 mm diam.; ovule sac 1.8–2.2 mm long; ovules 20–24(34) per locule, 2-seriate, contained within translucent, gelatinous ovule sac, 0.1–0.2 mm long, as long as or longer than funicle; funicle to 0.2 mm long, adnate to lower part of partition, style 0.5–0.6 mm long, 1.4–1.7 mm diam., similar to style type B; style apex ± flat; stigma ± lobed, 1.4 mm diam., 0.2–0.3 mm high, covering entire style apex; the androecium truncate, prismatic, oblong, margins ± 4–6-sided, 0.8–0.9 mm long, 2–2.5 mm diam. at apex; thecae oblong, 0.3–0.4 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregularly 4–5-sided, sometimes clavate or prismatic, 1.6–1.8 mm long, 1.4–1.7 and 1.9–3.4 mm wide. INFRUCTESCENCE with ripe berries white.

Flowering in *Philodendron verrucosum* occurs from April through June (also September and November) in Central America. The species probably also flowers earlier in the dry season, perhaps as early as February, as suggested by the fact that a post-anthesis collection was made in March (and even in February in Colombia). Post-anthesis collections have also been made from April through July (but also in December). Immature fruits have been seen from July, October, and December. The flowering collections from September and October, as well as the immature fruits from October and December, appear to reflect bimodal flowering. On the other hand, no flowers were seen from July and no flowers or fruits from August.

Philodendron verrucosum ranges from Costa Rica to Peru at 200 to 1500 (mostly above 500) m elevation, mostly in *Premontane rain forest* and *Tropical Lower Montane rain forest* but also in *Tropical wet forest.* In Central America, it occurs principally on the Atlantic slope or near the Continental Divide in Costa Rica and Panama but also on the Pacific slope in southwestern Costa Rica. In South America, it ranges along the Pacific slope of the Andes to as far south as El Oro and Cotopaxi Provinces in Ecuador, but also occurs on the eastern slopes of the Andes in Napo and Morona-Santiago as well as in Peru in the departments of San Martín and Junín at 750 to 1850 m elevation.

Philodendron verrucosum is a member of *P.* sect. *Philodendron* subsect. *Achyropodium.* This species is characterized by its short internodes, subterete petioles (about as long as the blades), broadly ovate-cordate blades velvety on the upper surface, and especially by the densely scaly or setose vestiture of the stems, cataphylls, petioles, and inflorescences.

Philodendron verrucosum might be confused with a few other species that have scaly parts, including

P. hammelii, P. malesevichiae, P. squamipetiolatum, and especially *P. squamicaule.* (See under the individual species for discussion of the differences.) *Philodendron squamipetiolatum* differs by its longer, more slender internodes and much smaller leaf blades (ca. 30 cm long on flowering plants) with a semi-glossy upper surface. It also differs in having solitary inflorescences (vs. usually more than one per axil in *P. verrucosum*). *Philodendron hammelii* differs in its much smaller size, petioles with foliaceous (rather than acicular) scales restricted to near the apex, and glabrous cataphylls, peduncles, and spathes. *Philodendron malesevichiae* differs by its terrestrial, creeping habit; persistent, semi-intact, glabrous cataphylls; narrowly sulcate petioles (rather than subterete as in *P. verrucosum*); and semiglossy blades lacking the conspicuous "crossveins" of *P. verrucosum.*

Additional specimens examined. COSTA RICA. **Alajuela**: Salto La Paz, 1350 m, *Ferreyra 15788* (USM); San Ramón–Balsa, ca. 2.3 km N Río Balsa, ca. 1050–1150 m, 10°11′N, 84°30′W, *Stevens 14194* (MO); ca. 4.6 km N of Río Balsa, 900–1000 m, 10°12′N, 84°31′W, *Stevens 13762* (CR, MO); 4–7 km N of Balsa, ca. 750 m, 10°13′N, 84°32′W, *Liesner & Judziewicz 14763* (MO); 2.5 km N of Balsa, 1050–1100 m, 10°11′N, 84°30′W, *Liesner & Judziewicz 14726* (CR, MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, ca. 850 m, *Croat 43636* (MO); 2 km N of Angeles Norte de San Ramón, 4000 ft., *Luteyn 3691* (MO); Zarcero–Quesada, 11.8 km past Zarcero, 1230 m, 10°12′N, 84°23′W, *Hoover 1352* (CR, MO); E of Río San Rafael, W of La Marina, 500 m, 10°23′N, 84°38′W, *Burger & Stolze 5041* (CR, US); Monteverde Biological Reserve, Río Peñas Blancas, 900 m, 10°18′N, 84°45′W, *Haber & Bello 8458* (CR, MO); 820 m, *Bello 2672* (CR); 850–900 m, *4478* (CR, INB); 950 m, *Bello & Méndez 2639* (CR, INB); Cantón Alfaro Ruiz, La Peña de Zarcero, *Smith 961* (F); Los Chiles–Los Angeles, San Ramón, 500–1200 m, 10°10′N, 84°30′W, *Barringer et al 2200* (CR, MO); *E. Schmidt 306* (CR). **Cartago**: 4000 ft., *J. D. Smith 391* (G); Moravia–Quebrada Platanillo, Moravia, 3–5 km from Finca Racine, 1200–1300 m, *Croat 36623* (MO); 1200–1400 m, *36795* (MO); Turrialba–Limón, along Hwy. 32, ca. 11 mi. NE of Turrialba, 850 m, *Croat 43355* (CR, MO); 31 km S of Siquirres on road to Turrialba (CR-101), 850 m, 9°57′N, 83°36′W, *Thompson & Rawlins 1163* (CM); El Muñeco, S of Río Navarro, 1400–1500 m, *Standley & Torres 51745* (CM, US); *Standley 33425* (US); Finca Navarro, 1350 m, *Maxon 636* (NY, US); 10 km S of Tapantí, 1600 m, 9°42′N, 83°46′W, *Burger & Burger 8424* (CR, F); 3.5 km SE of Tapantí, 1250 m, *Lent 851* (F, NY, US); Río Grande de Orosi, 2 km SE of Tapantí, 1350, *Lent 763* (F); 14 mi. from Turrialba, road to Pavones, *Carlson 3244* (F); Orosi, *Standley 39736* (US); La Estrella, *Standley 39547* (US); 4250 ft., *J. D. Smith 5963* (US); Río Gato, 4 km SE of Pejibaye, 700 m, 9°48′N, 83°42′W, *Liesner 14412* (MO); Tapantí Hydroelectric Reserve, 3–5 km from the gate, *D. Smith & Taylor 1009* (MO); 1300–1800 m, *Gómez 18889* (MO, RSA); Tapantí region, 1.5 km past Río Macho, along small stream along road to Humo, 1330 m, 9°17′N, 83°50′W, *Hoover 1345* (CR, MO); 4250 ft., *Cooper 5963* (CM, GH, US); Tucurrique, Las Vueltas, 635–700 m, *Tonduz 13321* (US); Reventazón Valley, Juan Viñas, *Cook & Doyle 288* (US). **Heredia**: 4 mi. N of Vara Blanca, 1350 m, *Croat 35609* (MO); 3 mi. S of Cariblanco, 760 m, *Croat 35794* (MO); La Selva Field Station, 280–300 m, 10°21′N, 84°03′W, *Schatz & Grayum 721* (DUKE). **Limón**: Cerro Chimú–Cerro Matama, 1200 m, *Gómez & Herrera 23533* (MO, US); Talamanca, Tsaki, 200 m, *Tonduz 9512* (CR, US); Fila Matama, 850 m, *Robles & Chacón 2724* (CR, MO). **Puntarenas**: Las Cruces Botanical Garden–Río Jaba, ca. 3 km SE of San Vito de Coto Brus, ca. 1050–1200 m, 8°47′N, 82°58′W, *Grayum 5621* (CR, MO); Monteverde Reserve, 1500 m, 10°17′N, 84°48′W, *Hammel & Zuchowski 13886* (MO). **San José**: San Isidro del General–Dominical, 4.8 mi. from Río Pacuare, 1000 m, *Croat 35251* (MO); 9 mi. SW of Río Pacuar, 680 m, *Croat 35349* (MO); Bijagual, 1300 m, *Gómez 20564* (M, MO, QCA); Alto San Juan, road to Dominical, 900 m, *Molina et al. 18096* (F, NY); La Hondura, 1300–1700 m, *Standley 37783* (US); Río Claro Valley (Bajo La Hondura), below La Palma, NE of San Jerónimo, 1000–1200 m, 10°3′N, 83°58′W, *Burger et al. 9433* (CR, F, U); below La Palma NE of San Jerónimo, 1000–1200 m, 10°3′N, 83°58′W, *Burger et al. 9386* (F, MO), *Burger & Gentry 9077* (CR, F); 1500 m, 10°3′N, 83°58′W, *Burger & Stolze 5308* (CR, F), *8499* (F); Tarrazú, vic. Hormiguero, 1100–1200 m, *Croat 78935* (INB, MO). PANAMA. **Bocas del Toro**: Cerro Colorado, 9.2 mi. W of Chame, 1450–1480 m, 8°35′N, 81°50′W, *Croat 69010* (MO); Fortuna Dam area, Chiriquí Grande–Gualaca, 21.4 km past Gualaca, 8°32′N, 82°19′W, *Hoover 1327* (MO); Continental Divide, ca. 1200 m, ca. 8°45′N, 82°15′W, *McPherson 9033* (CAS, CM, K, MO); *Croat 60374* (MO); Old Bank Island, vic. of Chiriquí Lagoon, *von Wedel 1923* (MO). **Chiriquí**: Volcán Cañas Gordas, 1 m E of Cañas Gordas, *Croat 22344* (MO); Cerro Colorado, 34.1 km beyond Río San Félix, 1390 m, *Croat 37254* (MO); Gualaca–Chiriquí Grande, vic. IRHE headquarters, 1200 m, 8°45′N, 82°18′W, *Croat 66719* (MO); *66558* (AAU, MEXU, MO, NY, PMA); road to Finca Landau, 1100 m, *Correa et al. 2141* (F, MO, PMA); NW of confluence of Río Hornito and Río Chiriquí, 1050–1100 m, 8°44′N, 82°13′W, *Sytsma & Stevens 2234* (MO, PMA); Fortuna Dam, Cerro Fortuna, lower slopes, 1150 m, *Knapp & Vodicka 5576* (MO); behind Vivero Forestal, 12 km N of Los Planes de Hornito, 1200–1300 m, 8°45′N, 82°12′W, *Knapp 4949* (MO); 7 km SE of Fortuna Dam, 1100 m, *O'Connor 91-512-004* (MICH); Continental Divide, 1200–1500 m, 8°47′N, 82°13′W, *Churchill 5298* (MO); 1200 m, *O'Connor 91-511-003* (MICH); Continental Divide trail, 1200–1300 m, 8°45′N, 82°15′W, *Thompson 4954* (CM, MO). **Coclé**: El Copé region, Alto Calvario, near Continental Divide, 5 mi. N of El Copé, 900–1000 m, 8°39′N, 80°36′W, *Croat 75058* (MO); 750–900 m, *44736* (MO); 8°39′N, 80°36′W, *68768* (CM, F, MO); El Valle region, La Mesa, *Gentry 5632* (MO, PMA); 860–900 m, *Croat 37339* (MO); *13341* (MO); 900 m, *Sullivan 544* (MO); *Liesner 756* (MO); NE slopes of Cerro Caracoral, N rim of El Valle, 2700–3200 ft., *Sytsma 3787* (MO); Cerro Pilón, 5 km NE of El Valle, 800–1045 m, *Mori et al. 6633* (MO); *Lallathin 5096* (MO); Cerro Gaital, 900–1000 m, 8°40′N, 80°07′W, *Knapp 5301* (MO); 800–900 m, *Knapp & Dressler 4913* (MO); 5.6 km S of El Valle, 870 m, 8°50′N, 80°07′W, *Hoover 1319* (MO, NY); ca. 3 km N of El Valle de Antón, 850 m, *Wilbur et al. 15656* (MO). **Darién**: Cerro Pirre region, 1000–1100 m, *Hartman 4829* (MO); 9–10 km N of Alto de Nique, 1520–1560 m, *Croat 37871* (MO); Río Tuquesa, vic. of Tyler

Kittredge gold mine, ca. 2 air km from Continental Divide, *Croat 27215* (MO). **Panamá**: El Llano–Cartí, 12 mi. above Pan-American Highway, 200–500 m, *Liesner 689* (MO); Campo Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Croat 22716* (MO); Cerro Campana, 1000 m, *Nee & Stockwell 11625* (MO); *Croat 17200* (MO); ca. 850 m, 8°40′N, 79°50′W, *Thompson 4576* (MO); 850 m, *Busey 875* (MO); above Su Lin Motel, *Croat 14728* (MO); near Florida State Univ. Building, *Croat 12121* (F, MO, SCZ). **San Blas**: Cerro Habú, vic. of peak, 2500 ft., 9°23′N, 78°49′W, *Sytsma et al. 2699* (MO, US); Cerro Brewster, 850 m, 9°18′N, 79°16′W, *de Nevers et al. 5546* (MO); Cerro Obu, 400–500 m, *de Nevers et al. 8053* (MO); Nusagandi, 310 m, 9°20′N, 79°W, *Croat & Zhu 76993A* (MO). **Veraguas**: Santa Fe region, NW of Santa Fe, 11 km from Alto Piedra, Río Dos Bocas Valley, 450–550 m, *Mori et al. 3815* (MO, PMA); NW of Santa Fe, along W fork of road beyond Alto Piedra, 0.6 mi. beyond fork in the road, 1300–1350 m, *Croat 49060* (MO); Santa Fe–Río Calovébora, 0.6 mi. beyond Alto Piedra, 735 m, *Croat & Folsom 33991* (MO); 1.7 mi. past Alto Piedra, 1.5 mi. beyond Quebrada Cosilla, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76856* (MO).

Philodendron warszewiczii K. Koch & Bouché, in A. Braun et al., Append. gen. sp. Hort. berol. 1855: 4. 1855–1856. TYPE: Guatemala. San José and Florida, *Warszewicz s.n.* (holotype, B? lost?). Guatemala. Santa Rosa: Volcán Jumaytepeque, 6000 ft., *Hyde & Lux 4282* (neotype, here designated, K). Figures 16, 441–444, 446–449.

Usually terrestrial, or on rocks, sometimes epiphytic; stem appressed-climbing, thick, succulent, bare, leaf scars conspicuous, 1.5–2.6 cm long, 1.5–2 cm wide; internodes short near apex, semiglossy, glaucous, 3–5(15) cm long, 2.5–7(10)cm diam., often longer than broad lower down, dark green to gray-brown; roots pale green to dark brown, few per node, epidermis drying yellowish; cataphylls thin, soft, 18–33 cm long, weakly to sharply 2-ribbed, pale green to whitish, lightly and densely short-lineate, deciduous intact. LEAVES often deciduous in dry season; **petioles** 33–58(80) cm long, 1–2 cm diam., subterete to C-shaped, moderately soft, weakly flattened to rounded with thick, medial rib adaxially, with adaxial margins sharply raised, surface sharply striate, with a dark green ring around apex; **blades** triangular-sagittate in outline, deeply bipinnately or bipinnatisect to within 1–4 cm of the midrib, thin, semiglossy, moderately bicolorous, ± rounded at apex (the acumen 2 mm long), cordate at base, 31–78 cm long, 30–62 cm wide (0.9–1.3 times longer than wide), (1–1.3 times longer than petiole), upper surface moderately glossy, moderately paler, margins sinuate; median lobe 17–52 cm long, 23–63 cm wide, rounded to obtuse; lateral segments 1–30 cm long, 11–28 cm wide, pinnately lobed with 3 or more lobes per side, acute or acuminate; interlobal sinuses 0.78–0.94 the length of the blades; midrib flat, obscurely striate, slightly paler than surface above, raised, obscurely striate, slightly paler than surface below; basal veins 2–6 per side, with 0–1 free to base, second and third pair coalesced 2–5 cm, third and higher order veins coalesced 5–7 cm; posterior rib naked along most of its margin; primary lateral veins 3–6 per side, departing midrib at a 55–70° angle, straight to the margins, weakly raised above, raised, paler than surface below; tertiary veins raised, paler than surface above and below; minor veins visible, darker than surface below, distinctly visible on drying, arising from both the midrib and primary lateral veins. INFLORESCENCES 1(3) per axil; peduncle (2.5–3)4.5–11(16) cm long, 1–2 cm diam., dark green, dark short-lineate; **spathe** 13.5–30 cm long, 4–7.5 cm diam. (1.1–3.6(4.7) times longer than peduncle), medium to dark green throughout, blunt at apex, scarcely constricted; spathe blade short dark green lineate outside, 12 cm long, pale green to white inside; spathe tube weakly short dark green lineate outside, 14 cm long, pale green to white or purple or red inside; **spadix** sessile; white throughout, 14–24(30) cm long, constricted weakly above pistillate portion; pistillate portion 3 cm long in front, 2 cm long in back, 1.3 cm diam. at apex, 1.7 cm diam. at middle, 1.6 cm wide at base; staminate portion 8.3–15 cm long; fertile staminate portion 1.6 cm diam. at base, 1.4 cm diam. at middle, 9 mm diam. ca. 1 cm from apex; sterile staminate portion 1.3 cm diam.; pistils (1.1)4.1 mm long, 3.5–4.5 mm diam.; ovary 4–5-locular, 2.6–9.5 mm long, 3.5–4.5 mm diam., with axile placentation; locules 2.6 mm long, 0.8–1.1 mm diam.; ovule sac 2.4 mm long; ovules 3–4 per locule, 0.5 mm long, contained in thick, translucent matrix; style 1.2–1.6 mm long, 1.2–1.4 mm diam., similar to style type E; style funnel broad, moderately deep; style apex ± flat; stigma subdiscoid, unlobed, 0.7 mm diam., 0.3 mm high, lining entire upper surface of funnel; the androecium truncate, prismatic, oblong, margins irregularly 4–6-sided, 3.3 mm long, 1.3 mm diam. at apex; thecae oblong, 0.4 mm wide, ± parallel to one another and nearly contiguous; sterile staminate flowers rounded to somewhat clavate, irregularly 4–6-sided, 2.6 mm long, 1.3–1.8 mm wide. INFRUCTESCENCE brownish outside, brownish inside, to 3 cm wide pistillate spadix 3–7.5 cm long; berries white, 8–11 mm long; seeds 3–4 per locule, pale yellow, oblong-ellipsoid, 2–2.5 mm long, 1–1.2 mm diam., with pale raphide cells.

Flowering collections of *Philodendron warszew-*

iczii are rare, known only from May. Post-anthesis collections, concentrated between April and June (but also January, February, March, July, August, September, and December), imply that the flowering period is relatively broad, perhaps throughout the entire dry season and the first half of the rainy season. Immature fruiting collections are scattered in a somewhat bimodal pattern, one group in the mid-rainy season from July through September, the other group primarily in the early dry season from December through March (especially December and January). The immature fruits collected in November might reflect an early dry season flowering. Mature fruits are known only from this same period between December and February at the beginning of the dry season.

Philodendron warszewiczii ranges from Mexico (Jalisco and Chiapas) to El Salvador on the Pacific slope, and to Honduras and Nicaragua at 300 to 1900 m elevation, in *Tropical dry forest* life zones. In Mexico, the species occurs in "Selva Mediana Subperennifolia" and "Selva Baja Caducifolia."

Philodendron warszewiczii is a member of *P.* sect. *Polytomium.* This species is distinguished by its moderately thin, deeply dissected, bipinnatifid leaf blades and thick, succulent stems often leafless during the dry season.

Philodendron warszewiczii is most similar to *P. radiatum* and *P. dressleri.* It differs from *P. radiatum* in having thinner, more highly divided blades and thicker stems. Although both species occur in some of the same forest types in Mexico, *P. radiatum* always occupies more mesic sites within these zones. In other parts of Central America for which there are Holdridge Life Zone maps, *P. radiatum* is found mostly in *Tropical moist forest* or wetter life zones, whereas *P. warszewiczii* is known from *Tropical dry forest* areas.

Although *Philodendron warszewiczii* and *P. dressleri* occupy equally dry sites, the latter is distinguished by occurring further north in Mexico and in having the leaves divided to no more than halfway to the midrib (vs. nearly all the way to the midrib in *P. warszewiczii*).

This species occurs principally on the Pacific slope except in Nicaragua (one Honduran collection is from the Atlantic slope). This is probably due to the fact that the Continental Divide runs very near the Pacific Ocean in Nicaragua, and because there is a second, generally much higher, more centrally located range of mountains and hills that creates a rain shadow throughout most of the Pacific side of the country. Because of this, *P. warszewiczii* inhabits many sites in the central part of the country well within the Atlantic watershed.

Common names for this species include: "Guacamayo," "Cupapayo," "Mano de Lión," "Copapayo," "Ocopayo," and "Papaya de Monte" (Standley & Steyermark, 1958b).

Additional specimens examined. EL SALVADOR. S of San Salvador, *Calderón 876* (GH, US). **Ahuachapán**: Ahuachapán vicinity, 800–1000 m, *Standley 19726* (GH, NY, US). **San Salvador**: *Calderón 416* (GH, NY, US); San Salvador vicinity, 650–850 m, *Standley 19624* (NY, US). GUATEMALA. **Jalapa**: Jalapa–San Pedro Pinula, 1400–1800 m, *Standley 77055* (F). **Jutiapa**: Monjas–El Progreso, above Ovejero, ca. 1400 m, *Standley 77660* (F); near Jutiapa, ca. 900 m, *60495* (F); Agua Blanca–Amatillo, 950–990 m, *Steyermark 30367* (F); Jutiapa–La Calera, SE of Jutiapa, ca. 850 m, *Standley 76087* (F). **Santa Rosa**: near Cuilapilla, ca. 900 m, *Standley 78051* (F). **Zacapa**: upper reaches of Río Sitio Nuevo, between Santa Rosalía and first waterfall, 1200–1500 m, *Steyermark 42281* (F); Río Lima, Sierra de las Minas, Finca Alejandria, 1500–1700 m, *Steyermark s.n.* (F). HONDURAS. Río de la Orilla, SE of El Zamorano, 900 m, *Anderson & Spoehr s.n.* (MO). **Comayagua**: vic. of Comayagua, ca. 600 m, *Standley & Chacón 6021* (F). **El Paraiso**: Danlí–Los Arcos, 740–850 m, *Standley 17007* (F); near Yuscarán, 960 m, *Standley et al. 1234* (F). **Morazán**: Tegucigalpa, Guarabuqui, 2600 ft., *von Hagen & von Hagen 1272* (F, NY); S. Antonio de Occidente, 850 m, *Valerio 3654* (F); Escuela Agrícola Panamericana, 800 m, *Croat 34814* (cultivated) (MO); San Antonio de Oriente, 4 mi. N of Zamorano, *Croat 42765* (MO, US); Río de la Orilla region, SE of El Zamorano, 900–950 m, *Standley 23205* (F), *23213* (F), *23217* (F); near El Zamorano, 800 m, *Morton 7119* (US). **Olancho**: Río Olancho, San Francisco de la Paz–Gualaco, 1–4 mi. NE of San Francisco de la Paz, 690–900 m, 14°57′N, 86°13′W, *Croat & Hannon 64186* (B, MO); W of main 8.6 mi. SW of Catacamas, 400 m, 14°45′N, 86°W, *Croat & Hannon 64136* (CM, MO). MEXICO. **Chiapas**: 20–30 mi. SW of El Jocote, on road to Motozintla, 700–900 m, *Croat 40714* (MEXU, MO); Tuxtla Gutiérrez–San Fernando, Chacona canyon, 850 m, *Breedlove 69987* (CAS); 22 mi. SE of Comitán, *Carlson 1953* (F); 6–8 km E of Frontera Comalapa, road to Ciudad Cuauhtémoc, 1000 m, *Breedlove 23428* (MO); 10 km E of Mozotintla, 1110–1150 m, *Garcia et al. 1527* (MEXU, BM); vic. Tuxtla Guttierez, 830 m, *Breedlove & Bourell 68505,* (CAS); Mpio. Tzimol, 15 km S of Comitán, 1200 m, *Breedlove 51028* (CAS). **Jalisco**: Autlán–Barra de Navidad, at km 291.67, ca. 300 m, *Moore & Bunting 8744* (BH); 9 mi. N of road-junction at W end of Bahía de Navidad, 300 m, *McVaugh & Koelz 1758* (MICH); Hwy. 110, 2 mi. NE of Huizache, ca. 5 m, *Stevens & Fairhurst 1823* (US); 15–16 mi. NW of Barra de Navidad, *Dressler & Wirth 2671* (UC, US); Chamela Field Station, 100 km S of Puerto Vallarta, 50 m, 19°30′N, 105°03′W, *Gentry 63966* (MO), *Bullock 1101* (MO); El Tejón, 100 m, 19°30′N, 105°03′W, *Gentry 74426* (MO); 10 km E of Las Palmas, 340 m, 20°50′N, 105°02′W, *Cochrane et al. 12022* (MO); Reserva Biosfera Sierra de Manantlán, Lagunillas–Juluapan, Cerro Grande, ca. 1400–1500 m, 19°22′N, 103°56′30″W, *Iltis et al. 29716* (MO); Rancho Cuixmala, Cumbres 1, Arroyo Cajones, 19°27′N, 104°58′30″W, *Lott et al. 3268* (MO). **Nayarit**: Mirador de Aguila, ca. 14 mi. N of Tepic, 450–600 m, *Feddema 824* (MICH); 6–7 mi. S of Com-

postela, 1000 m, *McVaugh 18754* (MICH); 2 mi. SE of Las Varas, road to Mazatlán, 60–90 m, *McVaugh 15351* (MICH). NICARAGUA. **Boaco**: Cerro Mombachito, 8.5 km NW of Camoapa, 1059 m, *Araquistain & Moreno 931* (MO); **Chontales**: 3.9 km N of Comalapa, ca. 460 m, ca. 12°18′N, 85°30′W, *Stevens & Montiel 17206* (MO); Juigalpa–La Libertad, ca. 17.4 km NE of Río Mayales, 350–400 m, 12°12′N, 85°17′W, *Stevens 4023* (MO). **Estelí**: 10 km S of Estelí, 1000 m, *Neill 1186* (MO); km 163 on Hwy. 1, ca. 11.2 km N of entrance to Estelí, ca. 920 m, ca. 13°13′N, 86°23′W, *Stevens 11213* (MO); Cerro Cucamonga, 800–850 m, 10°15′N, 86°22′W, *Moreno 14120* (MO); Salto de Estanzuela, ca. 5 km S of Estelí, 1000 m, 13°02′N, 86°20′W, *Guzmán et al. 1189* (MO); Río La Estanzuela, 6 km al S de Estelí, ca. 1000 m, 13°01′N, 86°21′W, *Moreno 9751* (MO). **Jinotega**: Jinotega–San Rafael, ca. 2 mi. NW of Jinotega, 1000 m, *Croat 43020* (MO); Lago de Abanas, 1–2 mi. E of San Rafael de Norte–Jinotega Road, 1000 m, *Croat 42970* (MO); ca. 1 mi. SE of Yalí, 850 m, *Croat 42891* (MO). **Madriz**: San Lucas–Hacienda El Volcán, 2 km NE de San Lucas, 800–900 m, 13°25′N, 86°35′W, *Araquistain & Moreno 2018* (K, MO); Cerro Volcán de Somoto (Tepesomoto), 900–1300 m, ca. 13°25′N, 86°35′W, *Stevens & Grijalva 16389* (MO); *Araquistain & Moreno 2046* (MO); ca. 7 mi. S of Ocotal, along Highway 15, 650 m, *Croat 42797* (MO). **Matagalpa**: 5–8 mi. E of Matagalpa, 800–1000 m, *Williams et al. 24048* (F); Cerro Apante, 1000–1400 m, *Moreno 155* (MO); 1 km SE of Matagalpa, 800 m, *Vincelli 297* (MO). **Nueva Segovia**: Cerro El Achiote, 7 km N of El Jícaro, 700–1000 m, 13°46′N, 86°08′W, *Araquistain & Moreno 2316* (MO, NY); Quebrada El Nancital, ca. 6.2 km N of Ocotal, Quebrada El Nancital, 700–760 m, ca. 13°41′N, 86°24′W, *Stevens 3040* (BM, MO); 6.5 km de Ocotal, road to Las Manos, ca. 700 m, 13°40′N, 86°29′W, *Moreno 14382* (MO); El Jícaro, "Casas Viejas," ca. 600 m, 13°44′N, 86°05′W, *Moreno 13504* (MO); El Jícaro, "El Cinchado," ca. 650–700 m, 13°46′N, 86°05′W, *Moreno 13589* (MO); El Jícaro, "Río Grande," road to Murra, 460–500 m, 13°43′N, 86°W, *Moreno 13670* (MO).

Philodendron wendlandii Schott, Prod. Syst. Aroid. 221. 1860. TYPE: Costa Rica. *Wendland s.n.* (holotype, W? lost). Schott ic. 2079 (neotype, here designated). Figures 15, 450, 451, 453.

Epiphytic, sometimes occurring high in the canopy, rarely terrestrial, perhaps by accident; stem short, scurfy, leaf scars inconspicuous, 1.3–2.1 cm long, 2–2.5 cm wide, obscured by root mass; internodes short, 0.5–3 cm long, 1.8–3.5 cm diam., glaucous, epidermis fissured transversely; roots reddish green becoming dark brown, blunt, branched near tip; cataphylls somewhat spongy or fleshy, 29–36 cm long, unribbed or sometimes sharply 2-ribbed, green to reddish green, persisting semi-intact at upper nodes, eventually fibrous. LEAVES rosulate; **petioles** 9–30 cm long, 1.5–4 cm diam., broader than thick, spongy, soft, sharply flattened adaxially, sharply convex abaxially, with adaxial margins erect on younger petioles, with dark green ring at apex; **blades** oblong-oblanceolate, coriaceous, slightly bicolorous, semiglossy, acuminate, sometimes long-acuminate at apex (the acumen inrolled, 2–4 mm long), ± narrowly rounded to obtuse at base, 32–67 cm long, 8.5–22 cm wide (2.6–4.7 times longer than wide), ((1.7)2.6–4.2(5.2) times longer than petiole), broadest ± near the middle; midrib flat to convex, broadly convex near base, convex toward apex, concolorous above, round-raised to convex, slightly paler than surface below; basal veins lacking; primary lateral veins 7–12(16) per side, departing midrib at a (50)60–70° angle, ± straight to the margins, weakly impressed to sunken above, convex to weakly raised, darker than surface below; minor veins obscure above, visible, darker than surface below, arising from midrib and paralleling primary lateral veins. INFLORESCENCES erect, 2 per axil; peduncle 3–10 cm long, 1–1.5 cm diam., pale green; **spathe** erect to erect-spreading, coriaceous, 12–18 cm long ((1.5)3.4–3.6(5.3) times longer than peduncle), constricted just above the tube to 2.1 cm diam. at constriction; spathe blade oblong-ovate, pale green to white, sometimes tinged pink, sometimes white-striate outside, 7–13 cm long, 2.6–7 cm diam. when open (opening broadly elliptic in face view, white (rarely rose-red)), pale-spotted with dark green central rib inside; spathe tube ellipsoid, pale to medium green, sometimes tinged with red, white-short-lineate in back outside, (3.5)5.5–7 cm long, 2.6–3.5 cm diam., pale green to white (sometimes creamy yellow or reddish with darker green central rib), minutely pale spotted inside; **spadix** stipitate to 1.3 mm long, light green; cylindrical, bluntly pointed at apex, (8.5)11–14.4(17.2) cm long, of nearly uniform width; pistillate portion pale green to yellowish green, cylindrical, or weakly tapered toward apex, 2.9–4.6(6.7) cm long, 1–1.2 cm diam. at apex, 1.1–1.4 cm diam. at middle, 1–1.5 cm wide at base; staminate portion 8.2–11.7 cm long; fertile staminate portion creamy white, with resin droplets, 9–13 mm diam. at base, 9–12 mm diam. at middle, 6–7(9) mm diam. ca. 1 cm from apex, broadest at the base or equally broad at base and middle, as broad as the pistillate portion, as broad as to slightly narrower than the sterile portion; sterile staminate portion slightly broader than the pistillate portion, white, 1–1.3 cm diam.; pistils 1.7–2.3 mm long, 1.4–1.7 mm diam.; ovary 6–7-locular, 0.7–1.3 mm long, 1.4–1.7 mm diam., with sub-basal placentation; locules 0.7–1.3 mm long, (0.2)0.4–0.5 mm diam.; ovule sac (0.7)1–1.1 mm long; ovules 2 per locule, translucent and contained within translucent or transparent ovule sac, 0.3–0.5 mm long, longer than funicle; funicle 0.2–0.4 mm long (can be pulled free to base), style 0.6–0.8 mm

long, 1.2–1.8 mm diam., similar to style type B; style apex sloping to weakly rounded, with depressions surrounding stylar canal exits; stigma subdiscoid, truncate, 0.7–1.1 mm diam., 0.2–0.3 mm high, covering center of style apex; the androecium truncate, prismatic, margins irregularly 3–6-sided, 1.2 mm long, 0.7–1.4 mm diam. at apex; thecae ± ovate, 0.5 mm wide, ± parallel to one another, sometimes nearly contiguous, sometimes distinctly contiguous; sterile staminate flowers blunt, irregularly 4–6-sided, sometimes clavate or prismatic, 1.4–1.6 mm long, 1.1–2(3.6) mm wide. Berries bright orange.

Flowering in *Philodendron wendlandii* occurs from the mid-dry season to the first part of the rainy season, with Costa Rican populations having been found in flower earlier (February and March) than those in Panama (May and June). Post-anthesis inflorescences have been collected between February and July, with an outlying collection from November. Immature fruits have been collected only in June and August, and mature fruits in September.

Philodendron wendlandii ranges from Nicaragua to Panama, from 10 to 1250 m elevation in *Tropical wet forest* and *Premontane rain forest* life zones. Most collections are from below 800 m elevation.

Philodendron wendlandii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Glossophyllum.* This species is distinguished by its true epiphytic habit, short stem, and rosulate, oblong-oblanceolate, short-petiolate leaves but especially by the petioles, which are often broader than thick and sharply flattened adaxially. *Philodendron wendlandii* is one of relatively few truly epiphytic, rosulate "bird's nest" species in the genus.

Philodendron wendlandii is apparently related to several species of more or less rosulate habit and with elongate leaf blades and a green or purple line of demarcation between the petiole and the blade. These include *Philodendron annulatum, P. auriculatum,* and *P. ligulatum.* With the exception of *P. ligulatum* var. *heraclioanum,* all of these taxa differ from *P. wendlandii* in having more or less terete petioles. *Philodendron ligulatum* var. *heraclioanum* itself differs in being a long-stemmed vine (vs. rosulate in *P. wendlandii*), and in having D-shaped petioles scarcely or not at all wider than thick (vs. sharply flattened and conspicuously broader than thick for *P. wendlandii*) and undulate-winged margins.

Additional specimens examined. COSTA RICA. **Alajuela**: near La Laguna, 6–8 km S of Villa Quesada, 1200 m, *Molina et al. 17553* (EAP, F, NY, US); Cañas–Upala, near Río Zapote, 1.8–2.7 km S of Río Canalete, 100 m, *Croat 36376* (MO); 8 km NE of Villa Quesada, 600 m, *Croat 46925* (MO); Río Frío, near Los Chiles, 30–40 m, 11°02′N, 84°44′W, *Holm & Iltis 826* (A, GH). **Cartago**: Moravia–Quebrada Platanillo, ca. 1250 m, *Croat 36683* (MO); 4 km S of Tucurrique, Río Vueltas, 690 m, *Lent 1096* (F). **Guanacaste**: El Silencio, near Tilarán, ca. 750 m, *Standley & Valerio 44785* (US). **Heredia**: 3 mi. S of Cariblanco, 760 m, *Croat 35833* (MO); S of Río Sarapiquí, opposite Chilamate, 60–100 m, 10°27′N, 84°04′W, *Grayum et al. 5311* (MO); La Selva Field Station, Puerto Viejo de Sarapiquí, 100–150 m, *Croat 44313* (MO); ca. 100 m, *Hammel 9086* (F, MO); *McDowell 943* (MO); *Folsom 9596* (TEX); *Hammel 8222* (DUKE). **Limón**: Finca La Suerte, *Davidson 3265* (MO); Hacienda Tapezco–Hacienda La Suerte, 29 air km W of Tortuguero, 40 m, 10°30′N, 83°47′W, *Davidson & Donahue 8599* (MO, RSA); *Croat 69732* (CM, MO); Hitoy–Cerere, Quebrada Cunabrí, Baja Talamanca, 500–800 m, *Gómez 24081* (MO); Amubri, along Río Lari, 200 m, 9°29′40″N, 82°89′40″W, *Herrera 2993* (AAU, CR, MO, US); Guápiles, 850 ft., *J. D. Smith 4977* (US); Cerro Coronel, E of Laguna Danto, 20–170 m, 10°41′N, 83°38′W, *Stevens 23863* (CR, MO); E of Laguna Danto, SW towards hills E of Río Zapote, 30–170 m, 10°40–41′N, 83°38–39′W, *Stevens et al. 24988* (CR, MO); E of Río Zapote, 1 km from Río Colorado, 10–40 m, 10°40′N, 83°40′W, *Stevens & Montiel 24313* (CR, MO); *Stevens et al. 24683* (CR, MO); between Río Madre de Dios and Quebrada Cañabral, 380–440 m, 10°02′N, 83°26′W, *Grayum et al. 8712* (CR); Parque Nacional Tortuguero, NE of La Aurora, Guápiles, along Río Sierpe, 30 m, 10°22′N, 83°31′W, *Robles 2254* (CR, MO). **San José**: Carrillo Station, 700 m, *Gómez et al. 21192* (CR, MO). NICARAGUA. **Río San Juan**: Bocas de Sábalo, 70–100 m, 11°03′N, 84°27′W, *Moreno 26780* (MO). PANAMA. **Bocas del Toro**: Fortuna Dam Area, Gualaca–Chiriquí Grande, 9.4 mi. N of the Continental Divide, 175 m, 8°46′N, 82°16′W, *Croat 66819* (K, MO); 2.8 mi. N of Continental Divide, 850–950 m, ca. 8°45′N, 82°15′W, *McPherson 9653* (L, MO, PMA, US). **Colón**: Cerro Bruja from Río Escandaloso, 2000 ft., *Hammel 3205* (MO); Santa Rita Ridge, Mile 10, *Porter et al. 4740* (MO); Mile 6.5, 370 m, 9°21′15″N, 79°44′W, *Croat & Zhu 76962* (MO). **Panamá**: Cerro Jefe region, Campo Tres, 3 mi. NE of Altos de Pacora, 500–800 m, *Croat 22721* (MO); 3–3.5 mi. NE of Altos de Pacora, 7.8–8.2 mi. above Pan-American Highway, 700–750 m, 9°15′N, 79°25′W, *Croat 68633* (MO); El Llano–Cartí, 10 mi. from main gate near El Llano, *Croat 33715* (CM, MO); Mile 10.1, Nusagandi, 300 m, 9°20′N, 79°W, *Croat & Zhu 76547* (MO). **Veraguas**: Santa Fe region, Santa Fe–Río Calovébora, 0.6 mi. N of Alto Piedra, 735 m, *Croat 34141* (MO); Santa Fe–Calovébora, 1.7 mi. past Alto Piedra, 1.5 mi. beyond Quebrada Cosilla, 570 m, 8°33′N, 81°08′W, *Croat & Zhu 76820* (F, MO).

Philodendron wilburii Croat & Grayum, sp. nov. TYPE: Costa Rica. Alajuela: Cordillera de Tilarán, San Ramón–Bajo Rodríguez, vic. La Balsa, 8.9 mi. NW of center of San Ramón, 1100 m, 10°10′30″N, 84°30′W, 26 Sep. 1987, *Croat 68083* (holotype, MO-3641132; isotypes, CR, K, US). Figures 452, 454–458.

Planta plerumque hemiepiphytica; caulis scandens; internodia 3–15 cm longa, 1.3–2 cm diam.; cataphylla 7–

26 cm longa, incostata vel obtuse 1-costata, decidua; petiolus subteres vel teres, moderate spongiosus, obtuse complanatus adaxialiter, 16–55 cm longus, 5–12 mm diam.; lamina ovato-triangularis, 17–36 cm longa, 11–31 cm lata, cordata vel sagittata basi; inflorescentia 1–3(4); pedunculus 3.5–29 cm longus, 8–12 mm diam.; spatha 7.5–18 cm longa; lamina spatha extus albida vel pallide viridi aut cremeo-flava, intus albida (sub anthesi) vel cremeo-flava; tubo spathae extus virenti, intus rubella vel atrimarronino; pistilla (5)6–7-loculari; loculi 1–2-ovulati; baccae pallide vel vivide aurantiacae.

Usually hemiepiphytic, sometimes terrestrial; stem scandent, semiglossy, sap watery, spicy-scented, sometimes milky-white; internodes usually long, glossy to semiglossy, 3–15 cm long, 1.3–2 cm diam., usually longer than broad, dark green to gray-green, sometimes drying black, epidermis often cracking or minutely fissured, brittle, sometimes silver-gray; cataphylls soft, 7–26 cm long, unribbed to bluntly or sharply 1-ribbed, sometimes sharply D-shaped and sharply 2-ribbed, whitish or green, fleshy, glossy, deciduous; **petioles** 16–55 cm long, 5–12 mm diam., subterete to terete, moderately spongy or moderately firm, bluntly D-shaped or obtusely flattened adaxially, surface weakly glossy to semiglossy, smooth; sheathing 6–8 cm long; **blades** ovate-triangular, thinly coriaceous to subcoriaceous, matte to semiglossy, weakly to moderately bicolorous, acuminate to long-acuminate at apex (the acumen more or less inrolled), cordate to sagittate at base, 17–36 cm long (averaging 26 cm), 11–31 cm wide, ± equal in length to or longer than petiole, margins hyaline, upper surface drying brownish, dark brown, or gray-brown to green, lower surface drying light brownish green to reddish brown or yellowish brown; anterior lobe 11.5–32 cm long, 7–24 cm wide; posterior lobes somewhat spreading, rounded to obtuse, 4–14 cm long, (2.7)4.2–13.5 cm wide, directed toward base or somewhat outward; sinus hippocrepiform, parabolic to arcuate or arcuate with petiole decurrent, 1–6(8) cm deep; midrib broadly convex to shallowly sunken to flat, paler than surface above, convex, paler than surface, drying darker than surface below; basal veins 3–5 per side, with 0–1 free to base, 1–3(4) coalesced (0.7)1.3–4(7) cm; posterior rib naked for 0.5–2.6 cm, sometimes not naked, directed to the tip of the posterior lobe 1–3.5 cm distant from the lower margin of the posterior lobe; primary lateral veins (2)3–4 per side, departing midrib at a 40–60(70°) angle, ± straight to the margins, streaked reddish below, broadly impressed to shallowly and obtusely sunken above, weakly convex and darker than surface below; minor veins moderately distinct, arising from both the midrib and primary lateral veins. INFLORESCENCES erect, 1–3(4) per axil; peduncle 3.5–29 cm long, 8–12 mm diam., medium green, glossy, faintly white-striate near apex; **spathe** glossy, 7.5–18 cm long, 1.4–2.2 cm diam., weakly constricted midway above the tube, 1.9–2.2 mm diam. at constriction; spathe blade creamy-white to pale green or creamy-yellow, sometimes tinged faintly reddish outside, 6–7 cm long, 2.2–3.2 cm diam. (opening 6.7–9 cm long, 3.2 cm wide), whitish (at anthesis) to creamy-yellow inside, sometimes suffused with red; resin canals orange and appearing as continuous lines at least around the throat inside; spathe tube medium to dark green and light maroon band near base, sometimes weakly to heavily tinged reddish (B & K red-purple 5/7.5), white-striate outside, 5–7.5 cm long, 2–3.6 cm diam., reddish to dark maroon (B & K red-purple 2/10) inside; **spadix** sessile; ± tapered toward apex, 6.7–11.1 cm long, broadest at or near the base, protruding strongly or weakly out of the spathe blade at anthesis; pistillate portion weakly tapered toward both ends, light green to yellowish green, (2.5)3.4–4.3 cm long in front, 2.9–3.8 cm long in back, 7–13 mm diam. at apex, 1–14 mm diam. at middle, 1–12 mm wide at base; staminate portion 5–8.4 cm long; fertile staminate portion white or light green, 10–11 mm diam. throughout, of nearly uniform diameter throughout or broadest in upper one-third, 9–13 mm diam. at base, 10–11 mm diam. at middle, 7–9 mm diam. ca. 1 cm from apex, broadest usually at the base, narrower than the pistillate portion, narrower than the sterile portion; sterile staminate portion as broad as the pistillate portion, (pre-anthesis) white to light gray, 9–14 mm diam.; pistils 1.1–2.3(3.5) mm long, 0.7–2 mm diam.; ovary (5)6–7-locular, 0.6–1.5(2) mm long, 0.8–1.3(1.6) mm diam., with sub-basal placentation; locules 0.7–1.1(2) mm long, 0.3–0.6 mm diam.; ovule sac 0.7–0.9 mm long; ovules 1–2 per locule, 2-seriate, contained within transparent, gelatinous ovule sac, 0.3–0.5 mm long, slightly longer than funicle; funicle 0.2–0.3 mm long (can be pulled free to base), style 0.3–1.2 mm long, 0.8–1.6 mm diam., similar to style type B; style apex flat to shallowly rounded or concave; stigma brushlike to discoid or subdiscoid, purplish violet or golden honey-colored, 1–1.5 mm diam., 0.2–0.4 mm high, covering ± entire style apex; the androecium truncate, prismatic, margins irregularly 4–6-sided, 1–1.7 mm long, 0.7–1.5(2.7) mm diam. at apex; thecae oblong, 0.4–0.5 mm wide, ± parallel to one another; sterile staminate flowers blunt, irregular, dense, 4–6-sided, prismatic, 1.5–2(2.5–3.3) mm long, (1.2)1.5–1.6(2) mm wide. Berries pale to bright orange (white, immature); seeds yellow-orange, narrowly ellipsoid.

Philodendron wilburii ranges from northern Costa Rica to the Canal Area of Panama from near sea level to 2000 m elevation. This species is highly versatile ecologically, ranging from *Premontane rain forest, Tropical Lower Montane wet forest,* and *Tropical Lower Montane rain forest* in the highlands to *Premontane wet forest* and *Tropical wet forest* life zones in the lowlands.

Philodendron wilburii is a member of *P.* sect. *Calostigma* subsect. *Glossophyllum* ser. *Ovata.* This species comprises somewhat scandent plants with elongate internodes drying grayish to yellowish brown and closely fissured; mostly 1-ribbed, deciduous cataphylls; subterete petioles mostly longer than the blades; ovate to ovate-triangular blades often with the lobes directed somewhat outward; and 1–3 prominently pedunculate white to greenish inflorescences per axil.

Philodendron wilburii is probably most closely related to *P. cotonense* from the mountains of eastern Costa Rica. That species is distinguished by its yellowish-brown-drying, more narrowly triangular blades averaging over two times longer than wide and thicker stems (2.5–3 cm diam. vs. up to 2 cm diam. in *P. wilburii*). It also has typically longer peduncles (mostly more than 10 cm) and more ovules per locule (4–5, vs. 1–2 in *P. wilburii*). The two species do not overlap in their distribution, but do occur in the same life zones.

Philodendron wilburii may be confused with *P. straminicaule* from Panama, but that species differs in having thicker and shorter internodes, 1-ribbed to sharply 2-ribbed cataphylls, and larger blades (rarely less than 35 cm long, vs. rarely more than 35 cm for *P. wilburii*), with frequently more than 6 basal veins and 6 primary lateral veins (vs. no more than 5 basal veins and mostly no more than 4 pairs of primary veins for *P. wilburii*). In addition, *P. straminicaule* frequently has the peduncle shorter than the spathe and has greenish white to lavender berries (vs. having the peduncle rarely shorter than the spathe and orangish berries in *P. wilburii*). *Philodendron wilburii* is also similar to *P. smithii,* which differs in having the dried stem epidermis conspicuously yellow-brown.

This species is named in honor of Robert Wilbur (DUKE), who has made major contributions to the study of Costa Rican plants and was one of the first to collect this species.

This species is here subdivided into two varieties.

KEY TO THE VARIETIES OF *P. WILBURII*

1a. Peduncles typically equal to or shorter than the spathe, usually less than 12 cm long; leaf blades with sinus hippocrepiform to parabolic, usually drying greenish to yellowish green below; Costa Rica (Alajuela, Cartago, Guanacaste, Heredia, Puntarenas, San José), 400–2000 m .... var. *wilburii*

1b. Peduncles typically much longer than the spathe, usually more than 12 cm long; leaf blades with sinus usually arcuate or arcuate with leaf tissue decurrent on petiole, rarely hippocrepiform, usually drying reddish brown below; Costa Rica (Cartago and Puntarenas) and Panama (Veraguas), 900–1400 m, 40–450 m along the Pacific slope ..... var. *longipedunculatum* Croat & Grayum

Philodendron wilburii Croat & Grayum var. **wilburii**

Usually hemiepiphytic, sometimes terrestrial; cataphylls 13–26 cm long, unribbed to bluntly 1-ribbed; **petioles** 16–46 cm long, obtusely flattened adaxially; blades ovate-triangular, cordate to saggitate at base, 17–36 (averaging 26) cm long, 11–27 (averaging 16) cm wide (1.3–2 times longer than wide, averaging 1.5 times), (1.3–2 times longer than petiole); sinus usually hippocrepiform, sometimes shallowly parabolic. INFLORESCENCE 1–3(4) per axil; peduncle 3.5–14 cm long; **spathe** 7.5–13.5 cm long; **spadix** 9–11 cm long; pistillate portion (2.5)3.4–4.3 cm long.

Flowering in *Philodendron wilburii* var. *wilburii* appears to have a bimodal pattern, with the main event occurring in the late dry season to the mid-rainy season (March through September but especially April through August). The second flowering event occurs in the early dry season, especially in January. A flowering collection from November is unusual. Post-anthesis collections also occur in two clusters, June through September and November through February. Mature fruits have been collected only in March.

Philodendron wilburii var. *wilburii* is largely known from central Costa Rica to an area of the frontier with Panama but rarely also to central Panama (Veraguas), extending from 400 to 2000 m, mostly at over 1000 m elevation. It is largely known from central Costa Rica, mostly at elevations of higher than 1000 m in premontane rain, lower montane wet, and lower montane rain forests. It has been collected mostly in the Cordillera de Tilarán, especially in the San Ramón region and in the Monteverde Reserve at 1350 to 1700 m (averaging at more than 1500 m) but to a lesser extent in areas to the east and west of the Central Valley. It has been collected only rarely in the Cordilleras de Guanacaste and Talamanca.

One collection believed to be this species, *Croat 76799,* is from Veraguas Province near Santa Fe in *Premontane moist forest.* Because of the isolated na-

ture of this population it may prove to represent a distinct taxon. The plants are unusual in having unribbed to bluntly 1-ribbed cataphylls; thin, ovate to ovate-triangular, cordate, mostly greenish-drying blades; and peduncles 3.5 to 14 cm long (averaging 9.3 cm long), usually equal to or shorter than the spathe.

Philodendron wilburii var. *wilburii* might be confused with a lowland form of *P. wilburii* var. *longipedunculatum* from southeastern Costa Rica that has leaf blades more nearly as broad as long (e.g., *Grayum 4759*). Especially confusing are *Grayum 4759* and *9167* from Puntarenas Province in the region of the Osa Peninsula at 300 to 400 m elevation. Both look much like *P. wilburii* var. *wilburii*, and if they prove to represent that taxon, they would be the only collections from such a low elevation and the only ones from southwestern Costa Rica.

Also noteworthy is *Croat 61199*, a sterile collection that had its locule and ovary number determined from a field-collected infructescence. This collection, from Monteverde in Puntarenas Province, Costa Rica, has ovaries with only 5 locules but 10–14 ovules per locule. It otherwise matches typical *P. wilburii*. Perhaps it represents a different species.

A collection from the Azuero Peninsula in Panama is somewhat intermediate between *P. wilburii* var. *wilburii* and *P. wilburii* var. *longipedunculatum*. Though it has very long peduncles like *P. wilburii* var. *longipedunculatum*, its blades dry somewhat blackened with the posterior lobes somewhat more rounded than normal for *P. wilburii* var. *longipedunculatum*.

Additional specimens examined for P. wilburii *var.* wilburii. COSTA RICA. **Alajuela**: San Ramón, N of Los Angeles, ca. 1200 m, *Primack et al. 236* (DUKE); between Los Angeles and ca. 4 km beyond Río Balsa, 1100–1200 m, *Utley 366* (DUKE); San Ramón–Bajo Rodriguez, 940 m, *Croat 78833* (CR, INB, MO); 1025–1100 m, *78885* (CR, INB, MO); San Ramón–Cataratas, km 11, 850 m, *Pennington 11543* (K); Cantón Alfaro Ruiz, Guadalupe, 1450 m, *A. Smith 2844* (F); San Luis de Zarcero, 1575 m, *A. Smith NY1023* (F, NY); 12 km NNW of San Ramón, 1100 m, 10°10′N, 84°29′W, *Liesner & Judziewicz 14913* (CR, MO, WIS); 15 km NNW of San Ramón by road, 2.5 km N of Balsa on road to San Lorenzo, 1050–1100 m, 10°11′N, 84°30′W, *Liesner & Judziewicz 14753* (MO); 17–20 km NNW of San Ramón, ca. 750 m, 10°13′N, 84°32′W, *14690* (MO, WIS); 1 km S of Balsa de San Ramón, 1200 m, 10°13′N, 84°31′W, *Lent 3514* (F, MO); 9 km SE of Ramón, 1000 m, 10°16′N, 84°05′W, *Loiselle 177* (MO); 11.2 km N of Zarcero, 1400 m, 10°12′N, 84°23′W, *Hoover 1351* (CR, MO); 5.7 mi. N of San Ramón, 1200 m, *Croat 46836* (MO); ca. 1.3 mi. N of Angeles Norte, ca. 1200 m, *Croat 46874* (MO); Finca Los Ensayos, ca. 11 mi. NW of Zarcero, *Croat 43634* (CM, MO); San Ramón–Balsa, ca. 5.7 km N of bridge over Quebrada Volio, 1100–1150 m, ca. 10°08′N, 84°29′W, *Stevens 14182* (CAS, MO); 2.3 km N, Río Balsa, ca. 1050–1150 m, 10°01′N, 84°30′W, *Stevens 14198* (K, MO); Reserva Forestal de San Ramón, ca. 10 km W of Laguitos, Río San Lorencito, 850–1100 m, 10°18′N, 84°34′W, *Hammel et al. 15252* (MO); 800–1000 m, 10°12′53″N, 84°36′28″W, *Herrera & Mora 179* (MO); Río San Pedro, Cerro Azahar, 15 km NW of San Ramón by air, 1400–1500 m, 10°09′30″N, 84°34–35′W, *Liesner et al. 15486* (MO), *15487* (CR, MO, NY, WIS); UCR Reserva, Fila Volcán Muerte, 1000–1300 m, 84°32′W, 10°12′N, *Barringer & Gómez-Laurito 2559* (F), *Barringer & Pérez 3784* (CR, F); Monteverde Reserve, *Dryer 794* (MO), *997* (F); 1500–1600 m, 10°17′N, 84°47′W, *Haber et al. 10069* (CR, MO, MV); 10°18′N, 84°47′W, *Grayum & Sleeper 3851* (CR, MO). **Cartago**: Moravia-Quebrada Platanillo, ca. 1250 m, *Croat 36658* (MO); SE of Turrialba, ca. 3 km NE of La Suiza, ca. 1200 m, *Lellinger & White 1403* (US); Tapantí Reserve, *Nilsson 195* (CR), *215* (CR), *220* (CR), *238* (CR), *254* (CR), *266* (CR), *367* (CR), *647* (CR); 1250–1350 m, *Ferreyra 15702* (USM); 1500–1800 m, 9°43′N, 83°47′W, *Grayum & French 5827* (INB, MO); ca. 1350 m, 9°47′N, 83°48′W, *Grayum & Sleeper 3694* (MO, US); *Utley & Utley 5613* (DUKE); 1500–1800 m, 9°43′N, 83°47′W, *Croat & Grayum 68292* (CR, MO, US); *Croat 36122* (MO); ca. 6 km S of Cartago by air, Quebrada Cangreja, 3 km S of Pan-American Highway, 1620–1650 m, 9°46′N, 83°57′W, *Liesner & Judziewicz 14474* (MO); Alto Patillos, 4 km S of Tapantí, 1480 m, *Lent 1240* (F); Río Grande de Orosi, ca. 15 km S of Tapantí, 1500 m, 9°42′N, 83°47′W, *Burger & Liesner 6752* (F, NY); La Sierra, 6 km NE of Empalme, 2000 m, *Gómez 19762* (MO); Santa Teresa–Río Coliblanco, 6–7 km NE of Pacayas, ca. 1700 m, *Luteyn 3246* (DUKE, MO); Quebrada Honda–Río Sombrero, ca. 1–2 km above El Muñeco, ca. 1400 m, *3236* (DUKE, MO); 31 km from San José, SE on CR-2, 1750 m, *Harmon 6105* (UMO); Río Grande de Orosi valley, near Río Villegas, 1700 m, *Lent 1860* (F); Río Macho, *Nilsson 242* (CR), *274* (CR), *312* (CR). **Guanacaste**: Tilarán, Z.P. Tenorio, 1050 m, *G. Rodríguez 24* (CR). **Heredia**: Río Peje–Río Sardinalito, Volcán Barva, 700–950 m, 10°17′30″N, 84°04′30″W, *Grayum 6929* (MO); Río La Paz Grande, 7.5 km N of Vara Blanca, 1270–1350 m, *Croat 36051* (MO); La Selva Field Station, *Valerio s.n.* (USJ). **Limón**: Kámuk massif, between Río Tararia and NE Kámuk páramo, 1900–2300 m, 9°14–15′N, 82°59′W, *Davidse & Herrera 29203* (CR, MO). **Puntarenas**: Monteverde Reserve, ca. 1350 m, *Croat 47139* (MO); 2 km SW Station, 1500–1550 m, *Ingram & Ferrell-Ingram 1734* (MO); ca. 3.5 km NE of Monteverde Reserve, ca. 1500 m, *Wilbur et al. 15816* (MO); *Kennedy 545* (F); *Haber 2369* (MO); *Pounds 321* (MO); *449* (MO); *Gentry et al. 48860* (CR, MO, NY); *Haber 3880* (MO); *Haber & Bello 2458* (MO); *Bello & Cruz 5237* (CR, INB); *Croat 61199* (MO); *Feinsinger et al. 83-66-1* (FLAS); *Burger & Baker 9649* (F, MO, SEL); Palmar Norte–Jalisco, 300–400 m, 8°58′30″N, 83°28′W, *Grayum et al. 9167* (MO). **San José**: Bajo La Hondura, Paracito–Río Claro, 1100–1400 m, *Croat 44494* (F, MO); above Río Hondura, at Baja La Hondura, 1150 m, *Taylor 17933* (NY); Cerro de la Muerte, along CA-2, N of turnoff for road 222, ca. 2000 m, *Croat 32851* (MO); ca. 15 km S of San Isidro de Cartago, 1880 m, *Utley & Utley 2948* (F); La Palma, ca. 1600 m, *Standley 38300* (US); La Palma area, 1400 m, 10°12′N, 84°10′W, *Burger & Liesner 6212* (CR, F, MO); ca. 6 km NE of San Jerónimo, *Primack et al. 322* (DUKE); Braulio Carrillo National Park,

1000–1500 m, 10°05′N, 83°57′W, *Croat 61227* (CM, MO); Río Patria–Río Zurquí, Cerro Hondura, 1500–1600 m, 10°04′N, 84°01′W, *Grayum & Sleeper 6116* (CR, MO); Puriscal, Z.P. La Cangreja, 500 m, *Morales 924* (CR, INB). PANAMA. **Veraguas**: vic. Santa Fe, along road between Santa Fe and Alto Piedra, 1.7 mi. N of Hotel Santa Fe, 470 m, 8°31′N, 81°05′W, *Croat & Zhu 76799* (B, CAS, CR, F, HMNM, K, MO, NY, PMA, SCZ, US).

Philodendron wilburii Croat & Grayum var. **longipedunculatum** Croat & Grayum, var. nov. TYPE: Costa Rica. Puntarenas: vic. of San Vito de Java, ca. 1 km S of San Vito on road to Villa Neily, 8°48′N, 82°57′W, 1100 m, 13 June 1987, *Croat 66169* (holotype, MO–3610645; isotypes, CR, K, NY, US). Figures 459–464.

Planta plerumque terrestris, interdum hemiepiphytica; caulis scandens; internodia 3–15 cm longa, 1.3–1.7 cm diam.; cataphylla mollia, 7–15 cm longa, acute D-formata, plerumque acute 2-costata, decidua; petiolus subteres vel obtuse complanatus adaxialiter, 16–55 cm longa, 5–10 mm diam.; lamina 22–35 cm longa, 16–31 cm lata, triangulari-ovata, lobis posticis angustis, patentibus; inflorescentia 1–2; pedunculus 11–29.5 cm longus, 5–10 mm diam., subteres; spatha 8.7–18 cm longa, saepe viridis omnino; lamina spathae extus viridi vel flaviviridi aut eburnea vel citrina, intus pallide viridi, cremea, albida aut suffusa rubra; tubo spathae extus virenti vel atriviridi, intus atrimarronino vel atripurpureo, rubro, rubriviolaceo aut violaceo; pistilla (5)6–7(8)-locularia; loculi 1–2-ovulati; baccae aurantiacae.

Usually terrestrial, sometimes hemiepiphytic; internodes 3–15 cm long, 1.3–1.7 cm diam.; cataphylls soft, 7–15 cm long, sharply D-shaped, usually sharply 2-ribbed, sometimes unribbed or sharply 1-ribbed; **petioles** 16–55 cm long, 5–10 mm diam., obtusely flattened or bluntly D-shaped adaxially; **blades** triangular-ovate with spreading lobes, 22–35 cm long (averaging 28 cm), 16–31 cm wide (averaging 21 cm; 1.03–1.4 times longer than wide, averaging 1.3 times), (0.6–1.3 times longer than petiole); sinus usually arcuate or arcuate with decurrent petiole. INFLORESCENCES 1 or 2 per axil; peduncle 11–29.5 cm long, 5–10 mm diam.; **spathe** 8.7–18 cm long; **spadix** 6.7–11.2 cm long; pistillate portion 2.8–5.5 cm long; ovary (5)6–7(8)-locular; ovules 1–2 per locule. Berries bright orange (mature) or white (immature); seeds yellow-orange, narrowly ellipsoid.

The flowering phenology of *Philodendron wilburii* var. *longipedunculatum* is poorly known. It appears to be bimodal or, in any event, unlike the pattern of any other species. All flowering collections have been made between September and April, in the late rainy season and throughout the dry season. However, post-anthesis flowering collections from July make it obvious that some flowering also takes place during June or July, perhaps both months. Other post-anthesis collections are from January through April and also in September. The only mature infructescence was collected in March.

Philodendron wilburii var. *longipedunculatum* is known principally from eastern Costa Rica and western Panama with an outlying population at Tapantí in Cartago Province, at 900 to 1400 m elevation, especially on the Atlantic slope but also on the Pacific slope at lower elevations (40 to 450 m). The Pacific coastal populations range from Carara to the Osa and Burica Peninsulas in Puntarenas Province, with outlying populations on the Azuero Peninsula and in the Canal Area of Panama.

Philodendron wilburii var. *longipedunculatum* is distinguished by the sharply two-ribbed, deciduous cataphylls; subterete, moderately firm petioles; typically triangular-ovate blades often drying reddish to yellowish brown and usually with narrow, spreading lobes; and very long-pedunculate inflorescences.

The highland populations differ from those of the lowlands in having longer posterior lobes, which are narrower and more prominently directed outward, averaging about 11 cm long (vs. about 8 cm long for the lowland populations). The lowland populations have proportionately narrower blades (owing to their lack of long, outward-directed lobes), averaging 1.6 times longer than wide (vs. 1.3 times for highland populations).

Lowland populations in the vicinity of the Burica Peninsula have somewhat thicker blades drying with a minutely pustular or granular lower surface with the secretory ducts mostly not visible. In contrast, blades of highland populations dry darker brown to almost blackened on the upper surface and are smooth on the lower surface with the secretory ducts clearly visible and alternating with the minor veins.

The Azuero population, represented by *Croat 34476*, has leaf blades that dry somewhat blackened and have posterior lobes somewhat less narrowed and less directed outward than those of the highland Chiriquí populations. The Canal Area populations, represented by *Croat 12351* and *Croat & Zhu 77083*, also differ in having proportionately longer petioles than material elsewhere. The latter collection is also exceptional in having four inflorescences per axil.

Grayum & Sleeper 3435 is a noteworthy collection from Tapantí, Cartago Province, Costa Rica. It is unusual both in being from well out of the normal range of the variety, but also in having narrower

leaf blades and shorter peduncles. Perhaps it represents another taxon.

Additional specimens examined. COSTA RICA. **Cartago**: Tapantí Region, N of Quebrada Casa Blanca, 1300 m, 9°47′N, 83°48′W, *Grayum & Sleeper 3435* (AAU, CR, MO). **Puntarenas**: San Vito–Ciudad Neily, Fila de Cal, ca. 500–620 m, 8°41′N, 82°56′30″W, *Grayum et al. 6048* (CR, INB, K, MO, PMA); Osa Peninsula, vic. Rincón de Osa, 250–540 m, 8°42′N, 83°31′W, *Croat & Grayum 59879* (CR, MO); Quebrada Banegas–Río Riyito, ca. 7 km W of Rincón de Osa, 100–300 m, 8°41′N, 83°33′W, *Grayum 4089* (CR, MO); Rincón–Aguabuena, road to Rancho Quemado, 100 m, 8°40′N, 83°31′W, *G. Herrera 4619* (CR, INB, MO); Finca Loma Linda, 1 mi. SW of Cañas Gordas, 1140 m, *Croat 22310* (F, MO); Río Piedras Blancas, Fila Costeña, Fila Cruces, Cerro Anguciana, 950–1150 m, 8°49′18″N, 83°11′15″W, *Grayum 10650* (CR, INB, MO); Quebrada Bonita, to ca. 1 km E of Costanera highway, Carara Reserve, 30–40 m, 9°47′N, 84°37′W, *Grayum 4759* (CR, L, MEXU, MO). **San José**: San Isidro de El General–Dominical, 4.8 mi. S of Río Pacuare, 1000 m, *Croat 35249* (CR, K, MO, PMA, US); ca. 0.5 mi. above turnoff to Canaán at Rivas, 900 m, *Croat 43429* (CR, MO); ca. 8 km SW of San Isidro de El General, 1000 m, *Williams et al. 28387* (F). PANAMA. **Bocas del Toro**: Fortuna–Chiriquí Grande, Continental Divide, 1200 m, 8°44′N, 82°17′W, *Croat & Grayum 60372* (COL, CR, DAV, IBE, K, MO, NY, PMA, S, U); 1.2 mi. N of Continental Divide, 910 m, 8°44′N, 82°17′W, *Croat 60454* (MO, PMA); 4.5–5 km N of dam over Fortuna Lake, 1100–1135 m, 8°43′N, 82°17′W, *Croat & Grayum 60026* (B, CAS, CR, F, L, KYO, MEXU, MO, NY, PMA, R, S); Cerro Colorado, ca. 7.5 mi. from Chame Camp, 1200–1250 m, ca. 8°35′N, 81°45′W, *McPherson 8868* (MO). **Canal Area**: Pipeline Road, near R. Agua Salud, *Croat 12351* (DUKE, F, MEXU, MO, SCZ); 6 mi. N of Gamboa, Río Mendoza, 9°11′N, 79°46′W, *Croat & Zhu 77083* (CM, CR, MO, NY). **Chiriquí**: Burica Peninsula, San Bartolo Límite, 18 km W of Puerto Armuelles, 450 m, *Busey 597* (CM, CR, MO); Rabo de Puerco, 8 km W of Puerto Armuelles, 50–150 m, *Croat 21958* (F, MO); 200 m, *22482* (F, MO); Cerro Colorado, 34–35.6 km above Río San Félix, 1390–1410 m, *Croat 37250* (F, MO, NY, PMA); 28 mi. above San Félix, 1200–1500 m, *33202* (MO); Gualaca–Fortuna, 10 mi. NW of Los Planes de Hornito, 1260 m, 82°17′W, 8°45′N, *Croat 50093* (L, MO, NY); 5.9 mi. NW of Los Planes de Hornito, 1370 m, 8°43′N, 82°15′W, *Croat 49852* (MO); 7.2 mi. beyond Los Planes de Hornito, 1165–1200 m, 8°44′N, 82°14′W, *67836* (CM, F, MO, PMA); 11.8 mi. N of Los Planes de Hornito, 1400 m, *48696* (MO); near Lago Fortuna, 1200 m, 8°46′N, 82°17′W, *Croat 74907* (MO, PMA); 1100–1200 m, 8°45′N, 82°18″W, *66565* (CM, MO); 4.8 mi. beyond IRHE Facilities at Dam, 8°46′N, 82°16″W, *Croat 68032* (MO, NY, PMA, US); trail to Río Hornito, 1100–1300 m, 8°45′N, 82°15′W, *Thompson 5003* (CM, MO); 8°45′N, 82°18′W, *Croat & Zhu 76416* (AAU, CAS, GB, MEXU, MO, SCZ, US); *76378* (MO, SCZ); N edge of lake, ca. 1100 m, ca. 8°45′N, 82°15′W, *McPherson 9081* (MO, US); 3.4 km N of Quebrada Chorro, 1.6 mi. N of center of bridge over lake, 1205 m, 8°43′N, 82°14′W, *Croat 74955* (MO); Finca Loma Linda, 1 mi. E of Cañas Gordas near Costa Rican border on road to Volcán, *Croat 23310* (F, MO). **Darién**: Parque Nacional Darién, W side of Cerro Pirre, 800–1,050 m, 7°56′N, 77°45′W, *Croat 69001* (MO). **Los Santos**: Azuero Peninsula, Jobero–Río Pedregal headwaters, 300–700 m, *Croat 34476* (MO, PMA). **Panamá**: Río Majé, ca. 4–5 mi. above waterfalls, near new Bayano Lake, <100 m, *Croat 34726* (MO).

Philodendron zhuanum Croat, sp. nov. TYPE: Panama. Coclé: Alto Calvario, vic. El Copé, ca. 6 km N of El Copé, 770 m, 8°38′N, 80°35′W, 12 July 1994, *Croat & Zhu 76755* (holotype, MO–4619357–9; isotypes, AAU, B, CAS, COL, CR, F, GH, K, MEXU, NY, PMA, QCNE, SCZ, US, VEN). Figures 465–468.

Planta hemiepiphytica; internodia 2–4 cm longa, 3–5.5 cm diam.; cataphylla 37–50 cm longa, acute 2-costata, decidua; petiolus 40–63 cm longus, obtuse D-formatus, in sicco manifeste complanatus usque 3–6 cm latus; lamina anguste ovato-sagittata, 38–62 cm longa, 27–32 cm lata; inflorescentia 3; pedunculus 9–14 cm longus, 1–1.5 cm diam.; spatha 13–18.5 cm longa, lamina spathae alba, intus suffusa magentea in triente inferiore; tubo spathae extus viridi, intus atriviolaceipurpureo; pistilla 8–9-locularia; loculi 1–3-ovulati.

Hemiepiphytic, loosely or appressed-climbing; leaf scars conspicuous, 3 cm long, 2 cm wide; internodes semiglossy, 2–4 cm long, 3–5.5 cm diam., dark green, drying dark brown, longitudinally wrinkled; roots drying light brown and weakly glossy, finely striate, epidermis peeling; cataphylls 37–50 cm long, sharply 2-ribbed, medium green, semiglossy, drying dark brown, deciduous; **petioles** 40–63 cm long (0.8–1.5 times longer than blades), bluntly D-shaped, faintly raised medially, moderately firm, medium green, surface dark green shortlineate, drying dark yellowish brown and glossy, prominently flattening to 3–6 cm wide and only a few mm thick, smooth to finely and closely striate; sheath 3–6 cm long, moderately closed; **blades** narrowly ovate-sagittate, moderately coriaceous, acuminate at apex, conspicuously sagittate at base, 38–62 cm long, 27–32 cm wide (1.8–2 times longer than wide), margins broadly undulate, much paler than surface, upper surface dark green, glossy, drying dark yellowish brown, lower surface weakly glossy, paler, drying reddish brown to yellowish green with conspicuous, dark intermittent secretory canals visible; anterior lobe 34–35 cm long, margins broadly convex, paler; posterior lobes 8.5–18.5 cm long, 7–13 cm wide, directed downward to slightly inward, broadly rounded; sinus narrow, spathulate to narrowly obovate, (7.5)15–19 cm deep, 1–3 cm wide; major veins drying with sharp ridges, usually darker than surface; midrib flat, paler than surface above, narrowly rounded, concolorous below; basal veins (3)5–6 per side, with the first free to base, numbers 3–5 coalesced (2)5–7 cm; posterior rib not at all naked or naked to 2.5 cm; primary lateral veins 6–7 per side, arising at an acute angle

then spreading to a 40–45° angle, weakly arcuate until near the margin, then turned up abruptly, weakly sunken above, convex, paler than surface below; minor veins clearly visible, arising from both the midrib and primary lateral veins, drying prominulous above, faint and weakly wrinkled below. INFLORESCENCES 3 per axil; peduncle 9–14 cm long, 1–1.5 cm diam., somewhat flattened, medium green, faintly short-lineate; **spathe** 13–18.5 cm long, margins paler; spathe blade white, except yellow-green medially on back side outside, tinged magenta on lower one-third inside; spathe tube medium green outside, dark violet-purple inside, **spadix** 11.5–18 cm long; pistillate portion creamy green, 3.5–8 cm long, 3–6 cm long in back, 1.5 mm diam. at apex, 1.9 mm diam. at middle, 1.8 mm wide at base; staminate portion 8–10 cm long; fertile staminate portion slightly narrower than the pistillate portion; sterile staminate portion barely distinguishable when fresh, 1.2–1.3 cm diam. at base, tapered only slightly upward when fresh (drying to 10 mm diam. at apex); pistils 1.9–2.1 mm long, 1.2–1.6 mm diam.; ovary 8–9-locular, 0.8 mm long, with basal placentation; locules 0.8–1.2 mm long; ovules 1–3 per locule, translucent, contained within gelatinous matrix (no true envelope), 0.3–0.4 mm long, equal in length to funicle, style similar to style type B; stylar canals emerging directly onto surface; style apex truncate; stigma short, covering entire style apex; the androecium truncate, margins irregularly 4–6 sided, 0.8–1.2 mm diam. at apex; sterile staminate flowers irregularly rounded, 0.8–1 mm wide.

Flowering in *Philodendron zhuanum* is documented by a single collection from July, at the beginning of the rainy season. A cultivated plant of the same collection flowered in November at the Missouri Botanical Garden.

Philodendron zhuanum is endemic to Panama in Coclé Province in an area of *Premontane rain forest* at 700 to 900 m elevation.

Philodendron zhuanum is a member of *P.* sect. *Calostigma* subsect. *Macrobelium* ser. *Macrobelium*. This species is distinguished by its short, thick internodes; deciduous, sharply two-ribbed cataphylls; bluntly D-shaped petioles about as long as the blades or slightly shorter; narrowly ovate blades with prominent posterior lobes, a narrow sinus and prominently visible secretory canals; up to three inflorescences per axil; and spathes green outside and whitish inside on the blade, and dark purple-violet inside on the tube.

Philodendron zhuanum is apparently related to *P. sagittifolium* and *P. aromaticum*, differing from both in having petioles which on drying become moderately spongiose, markedly flattened (especially in the middle portions), dark yellow-brown to yellowish, and often glossy. It also differs in having conspicuous secretory canals visible in both living and dried conditions. While secretory canals are present in both *P. sagittifolium* and *P. aromaticum*, they are quite inconspicuous.

This species is perhaps most easily confused with *P. aromaticum*, which has similar leaf blades with a naked posterior rib. The latter species occurs at lower elevations and nearer the coast. In contrast, *P. zhuanum* rarely has the posterior rib naked. While *P. zhuanum* has the spathe tube dark purple-violet inside with the same color bleeding onto the lower one-third of the blade, the spathe tube of *P. aromaticum* is white to weakly maroon within and the color does not merge onto the lower part of the blade.

Philodendron zhuanum is named in honor of Guanghua Zhu, my student, field companion, and a monographer of the genus *Dracontium*, who helped to collect the type and many other aroids during our fieldwork in Panama.

Additional specimen examined. PANAMA. **Coclé**: Alto Calvario, vic. El Copé, ca. 5 mi. N of El Copé, 900–1000 m, *Croat 75054* (CM, MO).

Nomen Incertae Sedis

Philodendron auritum Lindl., J. Hort. Soc. London 8: 60. 1853.

This is perhaps an older name for *Philodendron anisotomum* but was based on a cultivated plant collected by Skinner, perhaps in Guatemala, and no specimen or illustration is known to exist to confirm that it is even a *Philodendron*. Lindley stated that it had foliage very similar to a *Syngonium* illustrated by Vellozo (1825) in *Flora Fluminensis* (vol. 10, t. 113).

Excluded Names

Philodendron armigerum Standl. & L. O. Williams, Ceiba 3: 107. 1952. = *Syngonium armigerum* (Standl. & L. O. Williams) Croat, Ann. Missouri Bot. Gard. 68: 585. 1981.

Philodendron brevinodum Standl. & L. O. Williams, Ceiba 1: 231. 1951. = *Monstera tuberculata* Lundell var. *brevinoda* (Standl. & L. O. Williams) Madison, Contr. Gray Herb. 207: 92. 1977.

Philodendron hastiferum Standl. & L. O. Williams, Ceiba 1: 232. 1951. = *Syngonium hastiferum*

(Standl. & L. O. Williams) Croat, Ann. Missouri Bot. Gard. 68: 595. 1981.

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Appendix 1. Geographic Distribution of Central American *Philodendron* Subg. *Philodendron*.

	Mex	EN	Guat	EN	Beliz	EN	El Salv	EN	Hond	EN	Nic	EN	CR	EN	Pan	ECU	VEN	AMAZ	GUIANAS	BRAZIL	PERU	BOLIVIA	CUBA	TRINIDA
advena	1		1																					
albisuccus															1									
alticola													1		1									
angustilobum									1		1		1		1									
anisotomum	1		1				1		1				1		1									
annulatum															1									
antonioanum															1									
aromaticum													1	1										
auriculatum													1	1										
bakeri													1		1									
basii	1	1																						
breedlovei	1	1																						
brenesii													1		1									
brevispathum											1		1		1	1	1	1		1	1	1		
brewsterense															1									
brunneicaule													1		1	1								
chiriquense															1									
chirripoense													1	1										
clewellii															1									
coloradense															1									
copense															1									
correae															1									
cotobrusense													1	1										
cotonense													1		1									
crassispathum													1		1									
cretosum													1		1									
davidsonii subsp. davidsonii													1		1									
subsp. bocatoranum															1									
dodsonii													1			1								
dolichophyllum															1									
dominicalense													1	1										
dressleri	1	1																						
dwyeri					1	1																		
edenudatum															1									
ferrugineum															1									
findens													1		1									
folsomii															1									

Appendix 1. Continued.

	Mex	EN	Guat	EN	Beliz	EN	El Salv	EN	Hond	EN	Nic	EN	CR	EN	Pan	ECU	VEN	AMAZ	GUIANAS	BRAZIL	PERU	BOLIVIA	CUBA	TRINIDA
fortunense															1									
fragrantissimum			1		1				1		1		1		1		1	1	1	1	1		1	1
gigas															1									
glanduliferum subsp. gland.	1		1																					
grandipes											1		1		1	1								
granulare															1									
grayumii													1		1									
hammelii															1									
hebetatum															1	1								
hederaceum var. hederaceum	1		1		1		1		1		1		1		1	1	1	1	1	1	1	1	1	1
var. kirkbridei																								
var. oxycardium	1	1											1		1	1			1					
heleniae																								
immixtum															1									
jacquinii	1		1		1				1		1		1		1		1		1				1	
jefense															1									
jodavisianum	1		1		1				1		1		1		1	1	1							
knappiae															1									
lazorii															1									
lentii													1		1									
ligulatum var. ovatum															1									
ligulatum var. heraclioanum															1									
ligulatum var. ligulatum											1		1		1									
llanense															1									
madronense															1									
malesevichiae															1									
mexicanum	1		1						1				1		1									
microstictum													1	1										
morii															1									
niqueanum															1									
panamense															1									
pirrense															1									
platypetiolatum											1		1		1	1								
pseudauriculatum															1									
pterotum											1		1		1									
purpureoviride													1		1	1								

Appendix 1. Continued.

	Mex	EN	Guat	EN	Beliz	EN	El Salv	EN	Hond	EN	Nic	EN	CR	EN	Pan	ECU	VEN	AMAZ	GUIANAS	BRAZIL	PERU	BOLIVIA	CUBA	TRINIDA
purulhense	1		1																					
radiatum var radiatum	1		1		1		1		1		1		1		1									
var pseudoradiatum	1	1																						
roseospathum var roseo.															1									
var angustilaminatum															1									
rothschuhianum									1		1		1		1									
sagittifolium	1		1		1				1		1		1		1		1							
scalarinerve													1		1	1								
schottianum													1		1									
smithii	1		1		1				1		1													
sousae	1	1																						
squamicaule													1		1	1								
squamipetiolatum															1	1								
straminicaule													1		1									
strictum													1		1		1							
subincisum	1	1																						
sulcicaule													1		1									
tenue											1		1		1	1	1	1						
thalassicum													1		1									
tripartitum	1		1		1		1		1		1		1		1	1								
tysonii															1									
ubigantupense															1									
utleyanum															1									
verapazense	1		1																					
verrucosum													1		1	1		1			1			
warszewiczii	1		1				1		1		1													
wendlandii											1		1		1									
wilburii var wilburii													1		1									
var longipedunculatum													1		1									
zhuanum															1									
TAXON COUNT	21		15		9		5		13		18		48		82	16	8	5	4	3	4	2	3	2
ENDEMICS		7		0		1		0		0		0		6										
PERCENT ENDEMICS	33%		0%		11%		0%		0%		0%		13%		46%									
TOTAL SPECIES & SUBSPECIES	103																							
TOTAL SPECIES	95																							

Appendix 2. Technical Data on Pistils.

PHILODENDRON	Sect	LEAF BLADE	HABIT	STYLE	# LOCULES Min	# LOCULES Max	LOCULE LENGTH Min	LOCULE LENGTH Max	PLACENTATION	OVULES/LOCULE	Ovules/Locule Min	Ovules/Locule Max	OVULE LENGTH min	OVULE LENGTH max	OVULE LENGTH (mm)	ARRANG	ENVELOPE CONDITION
advena	CMM	cordate	c	B	6	7	1.30	7.00	sub	1–4	1	4	0.20	1.50	0.2-0.5 (1.5)	digittate	transl
albisuccus	PPA	cordate	c	B	5	6	5.40	5.40	axile	18–20	18	20			seeds	2-series	none
alticola	PPF	cordate	c	B	5	6	1.70	3.00	axile	12–18	12	18	0.40	0.50	0.4-0.5	2-series	none
angustilobum	TRI	3-lobed	c	B	7	8	0.90	1.20	sub	1 (2)	1	2	0.60	0.60	0.6		transp
anisotomum	TRI	3-lobed	v	B	7	8	2.70	3.20	sub	3 (4-5)	3	5	0.40	0.40	0.4	1-series	transl-gel
annulatum	CMM	oblong	c	B	7	8	0.90	2.50	sub	1-2(4-5)	1	5	0.30	1.70	0.3-1.7	1-series	transp
antonioanum	PPF	cordate	c	B	5	5	2.00	2.00	axile	25-30	25	30	0.4	0.4	0.4	2-3 series	none
aromaticum	CMM	cordate	c	B	9	10	1.80	1.80	sub	2–3	2	3	0.30	0.30	0.3	1-2 series	transl to transp
auriculatum	CGG	oblong	c	B	5	7	0.70	1.20	sub	(3)4	3	4	0.20	0.40	0.2-0.4	1-2 series	transp
bakeri	CGG	oblong	v	B	5	8	0.40	1.00	sub	1(2)	1	2	0.20	0.50	0.2-0.5		transp-gel
basii	CMP	cordate	c	D	4	6	2.00	2.00	sub	4–6	4	6	0.30	0.30	0.3	2-3 series	transp
breedlovei	PPF	cordate	c	B	5	6	0.30	0.30	axile	ca 20	20	20	0.30	0.4	0.3-0.4	2-3 series	none
brenesii	CME	cordate	c	B	6	7	1.80	1.80	sub	6–12	6	12	0.40	0.40	0.4	2-series	none-gel, matrix
brevispathum	PS	cordate	v	B	6	6	0.60	0.60	axile	6–14	6	14	0.30	0.4	0.3-0.4	2-3 series	none
brewsterense	CGG	ovate	v	D	5	5	0.60	0.60	sub	2	2	2	0.5	0.5	0.5		transp
brunneicaule	PPL	cordate	c	B	5	7	0.90	2.10	axile	(13)15-18	13	18	0.90	2.10	0.9-2.1	2-series	none
chiriquense	PPF	cordate	c	B	5	5	3.10	3.10	axile	ca. 14	14	14	0.60	0.60	0.6	2-series	none-gel, matrix
chirripoense	PC	ovate	v	B	4	6	1.40	1.40	axile	8–12	8	12	0.10	0.20	0.1-0.2	1-series	none
clewellii	CO	cordate	v	B	6	7	1.30	1.30	sub	2	2	2	0.20	0.20	0.2		transp
coloradense	CMM	cordate	c	B	4	5	1.80	1.80	axile	4–7	4	7	0.20	0.20	0.2	2-series	none-gel, matrix
copense	PPL	cordate	c	B	3	4			axile	20-22	20	22			seeds only	2-3 series	gel
correae	CGG	oblong	c/v	C	5	6	2.60	2.60	sub	1	1	1			seeds only		none
cotobrusense	TRI	cordate	c	B	6	7	1.10	1.10	sub	3	3	3	0.20	0.30	0.2-0.3	digittate	transp
cotonense	CGO	cordate	c	B	5	6	0.60	0.60	sub	4-5	4	5	0.10	0.10	<0.1	digittate	none
crassispathum	CME	subcord	c	D	6	7	5.00	8.00	axile	7-10	7	10	1.60	1.60	1.6	2-series	none
cretosum	PC	oblong	c	D	4	4	3.80	4.50	axile	20	20	20	0.20	0.60	0.2-0.6	2-3-series	none
davidsonii subsp davidsonii	CME	subcord	c	D	8	12	1.20	2.50	sub	4-8 (10)	4	10	0.20	0.60	0.2-0.6	2-series	transl
davidsonii subsp bocatoranu	CME	subcord	c	B	9	10	2.90	2.90	sub	6–12	6	12	0.40	0.40	0.4	2-series	transp
dodsonii	PPF	cordate	c	B	5	5	2.20	2.20	axile	20	20	20	0.30	0.40	0.3-0.4	2-series	none
dolichophyllum	CGG	oblong	c	B	7	9	1.00	2.80	sub	3–4	3	4	0.10	0.10	0.1	1-2 series	transp
dominicalense	CGO	cordate	c	B	5	6	0.70	0.70	sub	1	1	1	0.30	0.40	0.3-0.4		none-gel, matrix
dressleri	POL	cordate	c	B	4	5	2.50	2.50	axile	3-4	3	4	0.40	0.40	0.4	2-series	transl
dwyeri	CMM	cordate	c	D	7	8	0.70	0.70	basal	1	1	1	0.10	0.10	0.1		none
edenudatum	CMM	cordate	c	B	6	7	1.40	1.40	sub	3(4)	3	4	0.50	0.50	0.5	1-2 series	none-gel, matrix
ferrugineum	CMM	cordate	c	D	8	10	1.20	1.90	sub(axile)	2–4	2	4	0.40	0.50	0.4-0.5	1-series	none
findens	PPL	cordate	c	B	5	6	1.60	6.10	axile	15-20 (22)	15	22	0.30	0.50	0.3-0.5	2-series	none
folsomii	CGG	oblong	c	B	6	7	0.60	0.60	sub	1	1	1	0.20	0.30	0.2-0.3		none-gel, matrix
fortunense	PPL	cordate	c	B	7	8	1.90	1.90	sub	9–10	9	10	0.40	0.50	0.4-0.5	2-series	none
fragrantissimum	PM	cordate	c	D	7	9	1.60	2.30	axile	32-36	32	36	0.20	0.30	0.2-0.3	2-series	none-transp.
gigas	PPV	cordate	c	B	4	5	2.80	5.20	axile	20	20	20	0.10	0.10	0.1	2-3 series	none?
glanduliferum	PA	cordate	t	B	6	6	1.30	1.30	axile	10	10	10	0.50	0.50	0.5	2-series	none

Appendix 2. Continued.

PHILODENDRON	Sect	LEAF BLADE	HABIT	SYN	# LOCULES Min	# LOCULES Max	LOCULE LENGTH Min	LOCULE LENGTH Max	PLACENTATION	OVULES/LOCULE	Ovules/Locule Min	Ovules/Locule Max	OVULE LENGTH min	OVULE LENGTH max	OVULE LENGTH (mm)	ARRANG	ENVELOPE CONDITION
grandipes	PPF	cordate	t	B	5	6	1.00	1.50	axile	16-22	16	22	0.30	0.40	0.3-0.4	2-series	none
granulare	CGG	oblong	v	E	4	5			basal	1	1	1			seeds only		
grayumii	CMM	cordate	c	B	7	8	1.00	1.30	sub	(2)3-8	2	8	0.30	0.50	0.3-0.5	2-series	transp. gel. (none)
hammelii	PA	cordate	t	B	6	6	1.00	1.00	axile	14	14	14	0.10	0.20	0.1-0.2	2-series	gel
hebetatum	PPI	cordate	c	B	5	8	1.30	4.50	axile	18-24	18	24	0.20	0.20	0.2	2-series	none
hederaceum var. hederaceum	PS	cordate	v	B	4	6	8.00	8.00	axile	20-25	20	25	0.10	0.10	0.1	2-series	none
hederaceum var. kirkbrideı	PS	cordate	v	B	5	5	6.00	6.00	axile	20-25	20	25	0.10	0.10	0.1	2-series	none
hederaceum var. oxycardium	PS	cordate															
heleniae	CO	subcord	c/v	B	6	9	0.90	1.20	sub	(1)3-4	1	4	0.30	0.40	0.3-0.4	1-series	transl
immixtum	CGG	oblong	v	B	4	6	0.70	1.30	sub	1 (2)	1	2	0.40	0.70	0.4-0.7		transp
jacquinii	MAC	cordate	v	B	4	4	1.30	1.30	sub	2	2	2	0.60	1.00	0.6-1	2-series	none-gel. matrix
jefense	CMR	cordate	c	D	7	8	0.32	3.20	axile	6 seeds					seeds only	2-series	?
jodavisianum	PPF	cordate	c	B	4	6	1.20	1.70	axile	18-28	18	28	0.30	0.30	0.3	2-series	none
knappiae	CMM	cordate	c	B	4	4	0.80	0.80	axile	4	4	4	0.2	0.2	0.2	2-series	none?
lazorii	PPF	cordate	c	D	5	6	1.10	1.60	axile	10-14	10	14	0.30	0.30	0.3	2-series	none
lentii	CME	subcord	c/v	B	6	7	1.20	2.00	sub	(1-2) 4-6	1	6	0.30	0.50	0.3-0.5	1-2 series	transl
ligulatum var. ligulatum	CGG	oblong	c/v	B	6	8	0.80	2.40	sub	1	1	1	0.30	0.40	0.3-0.4		transl or gel
ligulatum var. heraclioanum	CGG	oblong	c	C	5	6	1.60	1.60	sub	2	2	2	0.40	0.50	0.4-0.5		none-gel. matrix
ligulatum var. ovatum	CGG	subcord	v	B	6	7	1.00	1.00	sub	2 (seeds)			0.4	0.4	0.4		transp
llanense	PPF	cordate	c	B	6	8	1.50	6.80	axile	(6)12-14(20)	6	20	0.20	0.30	0.2-0.3	1-2 series	transp-transl
madronense	TRI	3-lobed	c	D	6	7	2.30	2.30	sub	1	1	1			seeds only		transp
malesevichiae	PA	cordate	t	B	5	6	1.30	1.60	axile	20	20	20	.1	0.30	0.1-0.3	2-3-series	none
mexicanum	CMM	cordate	v	B	5	7	0.90	2.50	sub	1-2(3)	1	3	0.30	1.00	0.3-0.6(1.0)	digitate	transp
microstictum	CGO	subcord	v	B	6	7	0.80	0.80	sub	1	1	1	0.4	0.4	0.4		transl
morii	CGG	subcord	c	D	4	5	1.30	1.30	sub	1	1	1			seeds only		
niqueanum	CME	cordate	c						?	?					?	?	
panamense	PPF	cordate	c	B	4	6	1.00	3.00	axile	20-31	20	31	0.30	0.30	0.3	2-series	none
pirrense	PPF	cordate	c	B	5	6	1.70	1.70	axile	20	20	20	0.20	0.30	0.2-0.3	2-series	none
platypetiolatum	CMM	cordate	v	B	7	8	0.70	1.50	sub	3	3	3	0.20	0.50	(0.2)0.4-0.5	1-series	transp-transl
pseudauriculatum	CGG	oblong	c	B	6	8	1.40	2.10	sub	1-2 (4)	1	4	0.40	0.50	0.4-0.5	1-series	transp & gel
pterotum	PPL	cordate	c	B	6	6	1.50	1.90	axile	20	20	20	0.20	0.30	0.2-0.3	2-series	none?
purpureoviride	PS	cordate	v	D	4	5	6.20	6.20	axile	15-20	15	20	0.20	0.50	0.2-0.25	2-3-series	none
purulhense	PPF	cordate	c	D	6	7	5.00	5.00	axile	13-20	13	20	0.10	0.10	0.1	2-3-series	none
radiatum var. radiatum	POL	incis-lob	c	B(C)	5	7	1.90	6.50	axile	8	8	8	0.10	0.30	0.1-0.3	2-series	transl -gel
radiatum var. pseudoradiatum	POL	incis-lob	c	B	8	8	0.60	0.60	sub	3	3	3	0.30	0.30	0.3	1-series	transp
roseospathum var. roseospathum	PC	oblong	c	B	5	7	1.40	1.40	axile	14-18	14	18	0.30	0.50	0.3-0.5	2-series	none
roseospathum var. angustilaminatum	PC	oblong	c	D	4	4	1.10	1.10	axile	6–8	6	8	0.30	0.30	0.3	1-series	none
rothschuhianum	TRI	3-lobed	c	B	5	6	0.80	0.80	sub	1	1	1	0.30	0.50	0.3-0.5		transp to gel
sagittifolium	CMM	cordate	c	B	2	3	1.00	6.30	sub	2–4	2	4	0.10	0.50	0.1-0.5	1-2 series	transl-gel
scalarinerve	PPF	subcord	c	B	4	6	0.70	3.00	axile	(10) 12-14	10	14	0.30	0.40	0.3-0.4	2-series	none
schottianum	PPF	cordate	c	B	4	6	1.90	2.50	axile	10-14(16)	10	16	0.10	0.30	0.1-0.3	2-series	transl or transp

Appendix 2. *Continued.*

PHILODENDRON	Sect	LEAF BLADE	HABIT T	SEED I	SEED E	# LOCULES Min	# LOCULES Max	LOCULE LENGTH Min	LOCULE LENGTH Max	PLACENTATION	OVULES/LOCULE	Ovules/Locule Min	Ovules/Locule Max	OVULE LENGTH min	OVULE LENGTH max	OVULE LENGTH (mm)	ARRANG	ENVELOPE CONDITION
smithii	CGO	cordate	c	B		7	8	0.90	1.10	basal (sub)	1	1	1	0.30	0.40	0.3-0.4		transp
sousae	CMM	cordate	c	D		6	8	0.40	1.40	basal (sub)	2	2	2	0.10	0.20	0.1-0.2		transl, transp.,gel
squamicaule	PA	cordate	c	D		4	4	1.00	1.20	axile	20-28	20	28	0.20	0.20	0.2	1-2 series	none
squamipetiolum	PA	subcord	v	B		4	5	1.00	1.20	axile	20-30	20	30	0.10	0.20	0.1-0.2	2-3-series	none
steyermarkii	CGO	cordate	c	C		5	6	0.50	2.10	sub	1	1	1	0.20	0.30	0.2-0.3		sticky, transp
strictum	PPI	cordate	c	B		5	6	1.80	1.80	axile	20-28	20	28	0.20	0.40	0.2-0.4	2-series	none
subincisum	CMM	incis-lob	c	B		4	4	0.40	0.40	axile	16	16	16	0.40	0.40	0.4	2-series	transl
sulcicaule	CGO	cordate	c	B		4	5	0.40	0.40	sub	1	1	1	0.20	0.30	0.2-0.3		transl or transp
tenue	PPF	cordate	c	B		4	5	1.60	5.90	axile	12–14	12	14	0.40	0.40	0.4	2-series	none
thalassicum	PPI	cordate	c	B		5	7	2.00	4.90	axile	16-22	16	22	0.40	0.40	0.2-0.4	2-series	none
tripartitum	TRI	3-lobed	c/v	(B)(I		6	8	0.90	2.30	sub	1-2	1	2	0.40	0.60	0.4-0.6	1-series	none-gel. matrix
tysonii	CMR	cordate	c	B		6	8	0.80	1.30	sub	(4) 5-7	4	7	0.10	0.40	(0.1) 0.3-0.4	2-series	transp
ubigantupense	CGG	oblong	v	D		8	8	1.10	1.10	sub	1	1	1	0.3	0.3	0.3		transp
utleyanum	CGG	oblong	c	?		4	5			sub	1	1	1					?
verapazense	CMM	cordate	v	D		4	6	0.90	0.90	sub	2	2	2	0.4	0.4	0.4		transp & gel
verrucosum	PA	cordate	c	B		4	5	1.90	2.50	axile	20-24(32)	20	32	0.10	0.20	0.1-0.2	2-series	transp & gel
warszewiczii	POL	incis-lob	c	C		4	5	2.60	9.50	axile	3–4	3	4	0.50	0.50	0.5	1-2 series	thick transl matrix
wendlandii	CGG	oblong	c	B		6	7	0.70	1.30	sub	2	2	2	0.30	0.50	0.3-0.5		transp or transl
wilburii var wilburii	CGO	cordate	c/v	B		6	7	0.70	2.00	sub	1–2	1	2	0.30	0.50	0.3-0.5	1-series	transp-gel
wilburii var longipedunculatum	CGO	cordate	c/v	B		6	7	0.40	1.50	sub	1–2	1	2	0.20	0.60	0.2-0.3(0.6)	1-series	transp-gel
zhuanum	CMM	cordate	c	B		1	3	0.80	1.20	basal	1–3	1	3	0.30	0.40	0.3-0.4	1-series	gel matrix
			c = climber															
			v = vine															
			t = terrestrial															
											sum	324	439	11	16			
											count	46	46	44	44			
											average	7.04	9.54	0.24	0.37			

Code	Section	Subsection	Series
PPI =	Philodendron	Philodendron	Impolita
PPV =	Philodendron	Philodendron	Velvetina
PPF =	Philodendron	Philodendron	Fibrosa
PPA =	Philodendron	Philodendron	Albisuccosa
PM =	Philodendron	Macrolonchium	
PC =	Philodendron	Canniphyllum	
PPL =	Philodendron	Platypodium	
PS =	Philodendron	Solenosterigma	
PA =	Philodendron	Achyropodium	
CMM =	Calostigma	Macrobelium	Macrobelium

Code	Section	Subsection	Series
CME =	Calostigma	Macrobelium	Ecordata
CMR =	Calostigma	Macrobelium	Reticulata
CMP =	Calostigma	Macrobelium	Pachycaulia
CGG =	Calostigma	Glossophyllum	Glossophyllum
CGO =	Calostigma	Glossophyllum	Ovata
CO =	Calostigma	Oligocarpidium	
CB =	Calostigma	Bulaoana	
CE =	Calostigma	Eucardium	
TRI =	Tritomophyllum		
POL =	Polytomium		
MAC =	Macrogynium		

Appendix 3. Sectional Composition of *Philodendron* subg. *Philodendron* in Central America with number of species in Central America.

SECTION **BAURSIA**

Section 1. *Philodendron* sect. *Baursia* (Rchb. ex Schott) Engl. in Mart. Fl. bras. 3(2): 134. 1878 ..... None

SECTION **PHILOPSAMMOS**

Section 2. *Philodendron* sect. *Philopsammos* G. S. Bunting, Phytologia 60(5): 306. 1986 ..... None

SECTION **PHILODENDRON**

Section 3. *Philodendron* (Philodendrum) Schott
Subsection 1. *Macrolonchium* (Schott) Engl., Martius, Fl. Bras. 3(2): 139. 1878 ..... 1 sp.
Subsection 2. *Canniphyllum* (Schott) Mayo, Bot. J. Linn. Soc. 100. 168. 1989 ..... 3 sp., 1 subsp.
Subsection 3. *Platypodium* (Schott) Engl., Martius, Fl. Bras. 3(2): 137. 1878 ..... 5 sp.
Subsection 4. *Psoropodium* (Schott) Engl., Martius, Fl. Bras. 3(2): 138. 1878 ..... None
Subsection 5. *Solenosterigma* (Klotzsch ex Schott) Engl., Martius, Fl. Bras. 3(2): 139. 1878 ..... 3 sp., 3 subsp.
Subsection 6. *Philodendron.* ..... 20 sp.
Series 1. *Philodendron.* ..... None
Series 2. *Impolita* ser. nov ..... 3 sp.
Series 3. *Velveta* ser. nov ..... 1 sp.
Series 4. *Fibrosa* ser. nov ..... 15 sp.
Series 5. *Albisuccosa* ser. nov ..... 1 sp.
Subsection 7. *Achyropodium* (Schott) Engl., Martius, Fl. Bras. 3(2): 139. 1878 ..... 6 sp.

SECTION **CALOSTIGMA**

Section 4. *Calostigma* (Schott) Engl., Martius, Fl. Bras ..... 48 sp., 4 subsp.
Subsection 1. *Macrobelium* (Schott) Engl., Martius, Fl. Bras. 3(2): 143. 1878.
Series 1. *Macrobelium.* ..... 16 sp.
Series 2. *Ecordata* ser. nov ..... 5 sp., 2 subsp.
Series 3. *Reticulata* ser. nov ..... 2 sp.
Series 4. *Pachycaulia* ser. nov ..... 1 sp.
Subsection 2. *Glossophyllum* (Schott) Croat, comb. nov.
Series 1. *Glossophyllum* Schott ..... 15 spp., 3 subsp.
Series 2. *Ovata* ser. nov ..... 7 spp., 2 subsp.
Subsection 3. *Oligocarpidium* Engl., Engler's Bot. Jahr. 26: 535. 1899 ..... 2 spp.
Subsection 4. *Bulaoanum* Mayo, Bot. J. Linn. Soc. 100: 168. 1989 ..... None
Subsection 5. *Eucardium* (Engl.) Mayo, Bot. J. Linn. Soc. 100: 168. 1989 ..... None

SECTION **TRITOMOPHYLLUM**

Section 5. *Tritomophyllum* (Schott) Engl., Martius, Fl. Bras. 3(2): 144. 1878 ..... 6 spp.

SECTION **SCHIZOPHYLLUM**

Section 6. *Schizophyllum* (Schott) Engl., Martius, Fl. Bras. 3(2): 144. 1878 ..... None

SECTION **POLYTOMIUM**

Section 7. *Polytomium* (Schott) Engl., Martius, Fl. Bras. 3(2): 145. 1878 ..... 3 spp., 2 taxa

SECTION **MACROGYNIUM**

Section 8. *Macrogynium* Engl., Bot. Jahrb. 26: 553. 1899 ..... 1 sp.

SECTION **CAMPTOGYNIUM**

Section 9. *Camptogynium* K. Krause, in Engler, Das Pflanzenreich IV. 23Db (Heft 60): 3, 127. 1913 ..... None

Appendix 4. Phenological Patterns of Central American *Philodendron* subg. *Philodendron*.

	Flowering Pattern						
PHILODENDRON	All Year	Wet	Wet->Dry	Dry	Dry-> Wet	BiModal	Unknown
advena	1						
albisuccus		1					
alticola					1		
angustilobum					1		
anisotomum			1				
annulatum					1		
antorianum		1					
aromaticum						1	
auriculatum					1		
bakeri				1			
basii		1					
breedlovei		1					
brenesii					1		
brevispathum					1		
brewsterense				1			
brunneicaule					1		
chiriquense		1					
chirripoense				1			
clewellii					1		
coloradense		1					
copense						1	
correae		1					
cotobrusense		1					
cotonense					1		
crassispathum					1		
cretosum					1		
davidsonii subsp. davidsonii					1		
subsp. bocatoranum+A50		1					
dodsonii		1					
dolichophyllum					1		
dominicalense		1					
dressleri		1					
dwyeri				1			
edenudatum				1			
ferrugineum		1					
findens					1		
folsomii				1			
fortunense					1		
fragrantissimum					1		
gigas		1					
glanduliferum subsp. glanduliferum		1					
grandipes					1		
granulare		1					
grayumii					1		
hammelii		1					
hebetatum					1		
hederaceum var. hederaceum	1						
var. kirkbridei					1		
var. oxycardium							1
heleniae					1		
immixtum					1		
jacquinii		1					

Appendix 4. Continued.

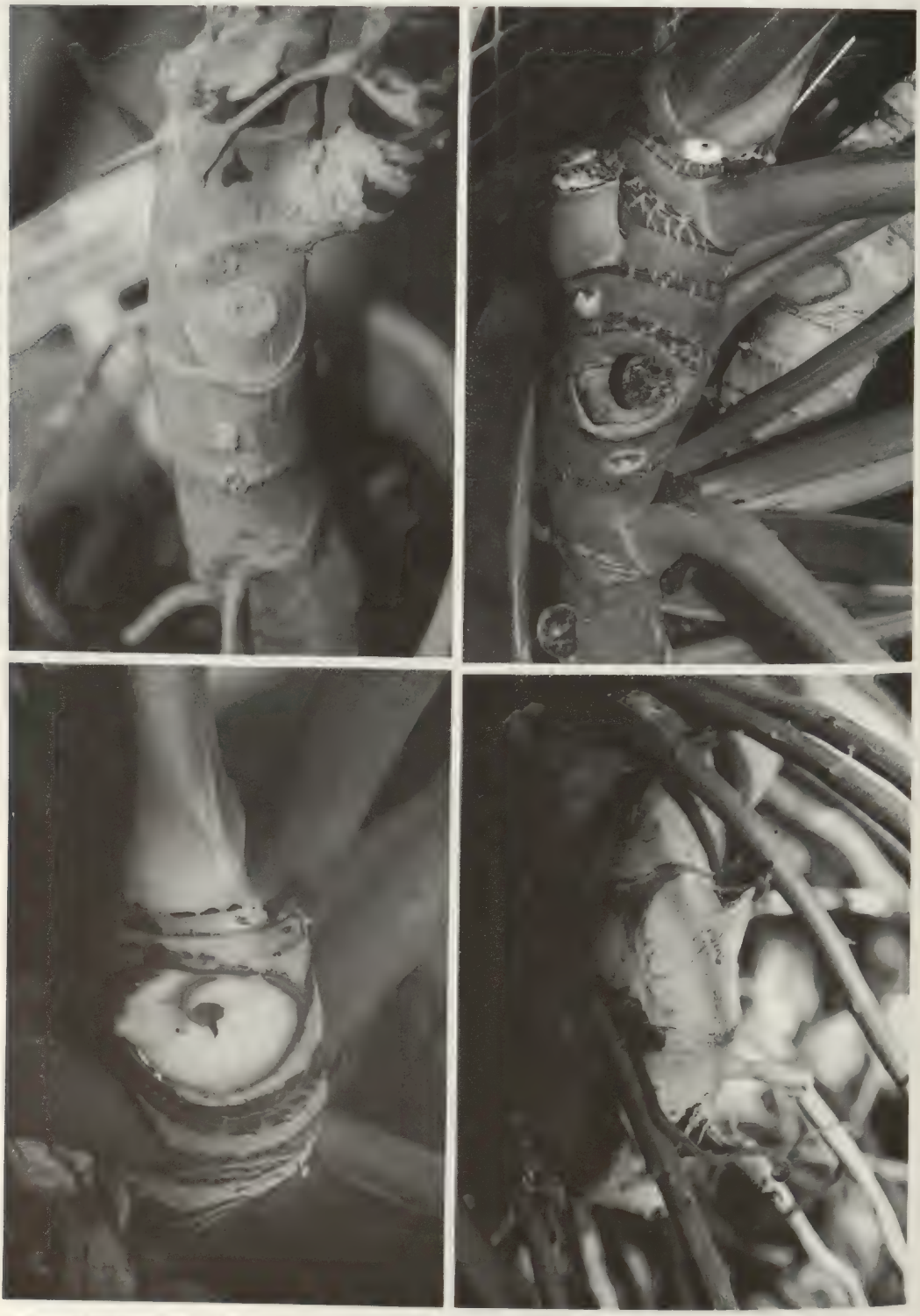
	Flowering Pattern						
PHILODENDRON	All Year	Wet	Wet->Dry	Dry	Dry-> Wet	BiModal	Unknown
jefense		1					
jodavisianum					1		
knappiae				1			
lazorii					1		
lentii					1		
ligulatum var. ligulatum							1
var. heraclioanum							1
var. ovatum							1
llanense					1		
madronense		1					
malesevichiae					1		
mexicanum					1		
microstictum					1		
morii						1	
niqueanum		1					
panamense					1		
pirrense		1					
platypetiolatum					1		
pseudauriculatum					1		
pterotum					1		
purpureoviride	1						
purulhense		1					
radiatum var radiatum	1						
var pseudoradiatum	1						
roseospathum var roseospathum					1		
var angustilaminatum		1					
rothschuhianum					1		
sagittifolium					1		
scalarinerve					1		
schottianum					1		
smithii					1		
sousae		1					
squamicaule		1					
squamipetiolatum					1		
straminicaule					1		
strictum					1		
subincisum							1
sulcicaule					1		
tenue					1		
thalassicum					1		
tripartitum					1		
tysonii					1		
ubigantupense		1					
utleyanum		1					
verapazense					1		
verrucosum					1		
warszewiczii					1		
wendlandii					1		
wilburii var wilburii						1	
var longipedunculatum			1				
zhuanum		1					
TOTAL	5	29	2	7	51	4	5

Appendix 4. Continued.

	Flowering Pattern						
PHILODENDRON	All Year	Wet	Wet->Dry	Dry	Dry-> Wet	BiModal	Unknown
% of Total	4.85%	28.16%	1.94%	6.80%	49.51%	3.88%	4.85%

Figures 1–4. —1 (top L). *Philodendron radiatum*, showing adventitious roots. Cultivated at Summit Gardens. —2 (top R). *P. schottianum* (*Croat 66395*), showing stems with transverse fissures and coarse striations at apex of node. —3 (bottom L). *P. malesevichiae*, showing trichome-like scales (*Croat 76707*). —4 (bottom R). *P. rothschuhianum*, showing stems that dry with minute cracks and scurfy condition (*Croat 57199*).

Figures 5–8. —5 (top L). *Philodendron conforme* (Venezuela), showing stems with transverse fissures at points of stress, petiole scar, and scar of inflorescence (*Croat 59355*). —6 (top R). *P. straminicaule*, dried stem showing conspicuous ribbing caused by drying (*Croat & Grayum 60057*). —7 (bottom L). *P. findens*, dried stem showing interruption of conspicuous epidermis by petiole base (*Croat 66811*). —8 (bottom R). *P. radiatum* Schott var. *pseudoradiatum*, showing stems with cracking and protruding epidermis (*Croat & Hannon 63381*).



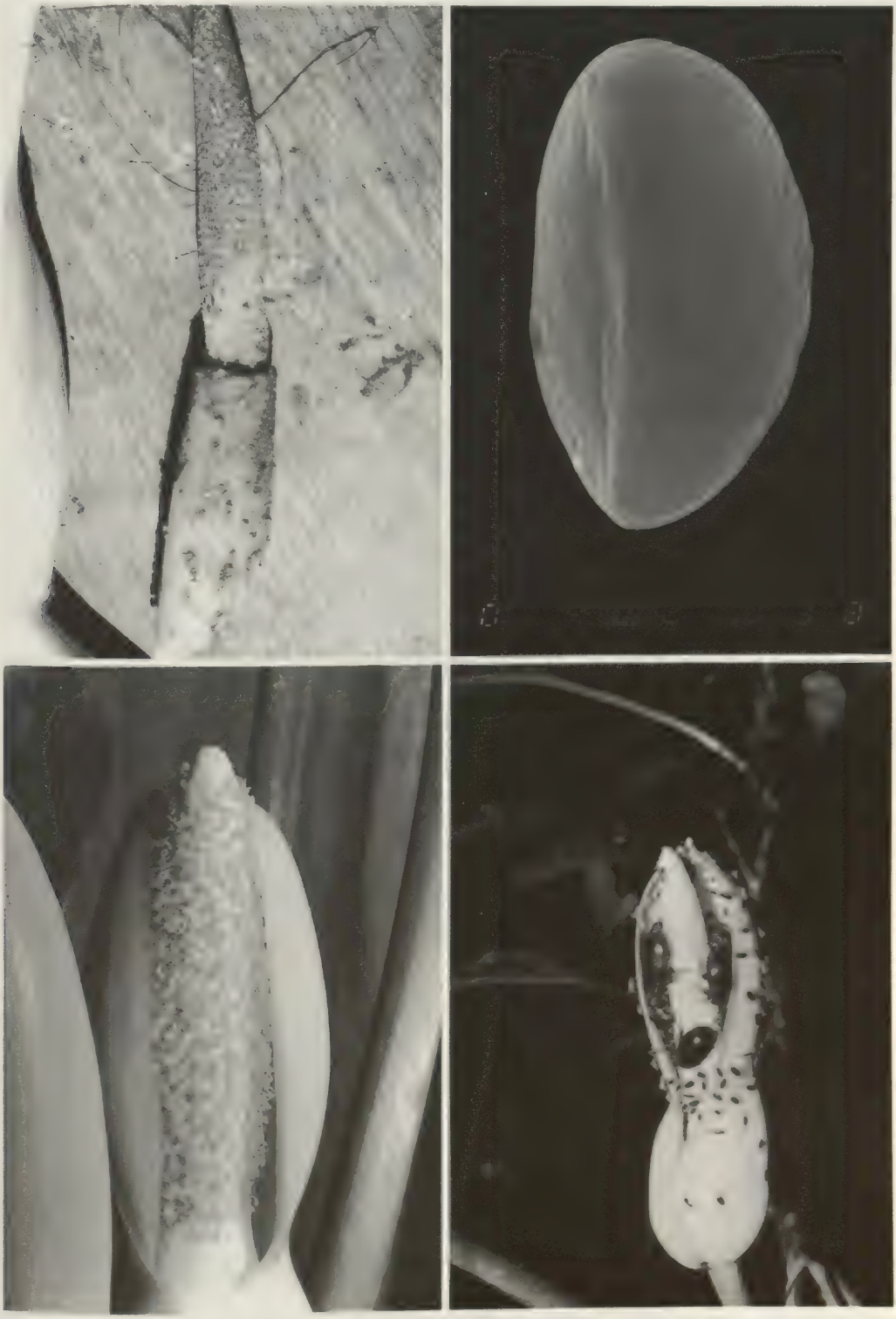
Figures 9–12. —9 (top L). *Philodendron rothschuhianum*, showing inconspicuous cataphyll scars and petiole scars (*Croat 57199*) (photo: P. Malesevich). —10 (top R). *P. davidsonii* (*Davidson 3956*), showing stem with conspicuous cataphyll scars and petiole scars. —11 (bottom L). *P. megalophyllum* (*Croat 54252*), stem with intravaginal squamulae occurring just above the cataphyll scar. —12 (bottom R). *P. auriculatum* (*Croat 59730*), stem with spreading anchor roots showing spinelike root branch buds.

Figures 13–16. 13, 14. *Philodendron lazorii* (*Croat 69833*). —13 (top L). Showing clasping roots closely appressed to tree. —14 (top R). Showing clasping roots and a much larger feeder root. —15 (bottom L). *P. wendlandii*, showing persistent, intact cataphylls held in place by contiguous petioles (*Croat 69732*). —16 (bottom R). *P. warszewiczii*, showing weakly 2-ribbed, short-lineate cataphyll (*Croat & Hannon 64186*).

Figures 17–20. —17 (top L). *Philodendron schottianum*, showing bluntly 2-ribbed cataphyll (*Croat & Zhu 76518*). —18 (top R). *P. megalophyllum*, showing petioles which are narrowly sulcate with broadly rounded margins (*Croat 54252A*). —19 (bottom L). *P. davidsonii* subsp. *bocatoranum*, showing sweet, viscid droplets and combination of short-lineate and lineate-streaked markings (*Croat 38177*). —20 (bottom R). *P. auriculatum*, showing dark green ring demarcating petiole and blade and free basal veins (*Croat & Grayum 59730*).

Figures 21–24. —21 (top L). *Philodendron maleseruchiae*, showing snapped petiole with slender strands of latex (*Croat & Bay 75810*). —22 (top R). *P. giganteum* (*Croat 68568*), showing midrib, primary lateral veins, and basal veins (the lowermost primarily fused to form posterior rib). —23 (bottom L). *P. auriculatum*, showing quilted primary lateral veins (*Croat & Grayum 59730*). —24 (bottom R). *P. megalophyllum*, showing arrangement of veins: midrib, primary lateral veins with lowermost branching (these secondary veins), and interprimary veins (*Croat 53901*).

Figures 25–28. —25 (top L). *Philodendron malesevichiae*, showing lowermost primary lateral veins and basal veins (these loosely coalesced toward the base) (*Croat 74818*) (photo: P. Malesevich). —26 (top R). *P. megalophyllum*, showing minor veins arising from the midrib and primary lateral veins (*Croat 53901*). 27, 28. *P. malesevichiae* (*Croat & Zhu 76707*). —27 (bottom L). Fresh spadix with pistillate flowers at base, sterile staminate flowers in middle, and a portion of the fertile staminate spadix at apex. —28 (bottom R). Older spadix showing the discolored staminate spadix and white sterile staminate portion.



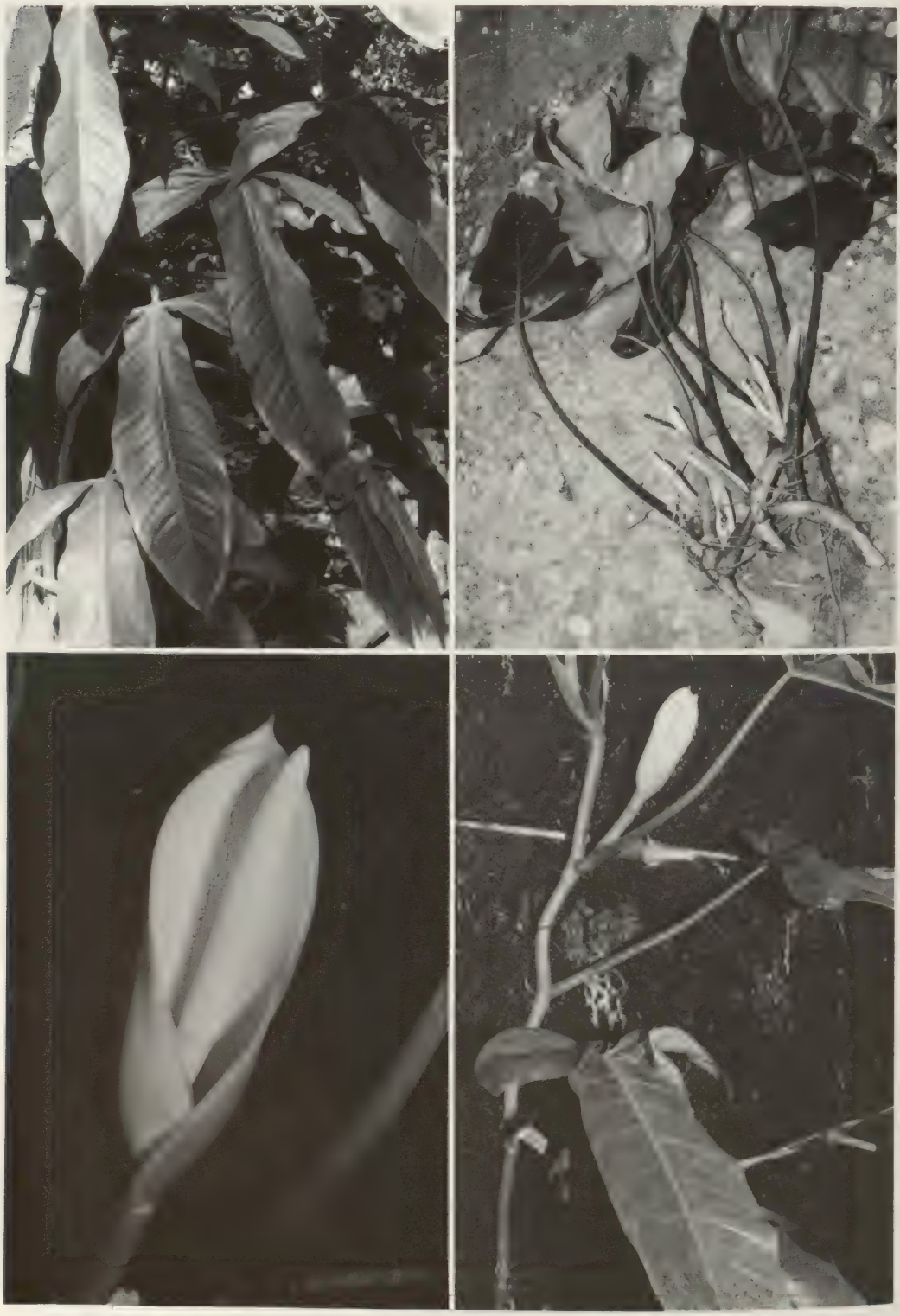
Figures 29–32. —29 (top L). *Philodendron tysonii*, showing spadix with sterile male flowers having been consumed by beetle pollinators (*Croat 67577*). —30 (top R). *P. fragrantissimum*, pollen grain (*Grayum 2436*, DUKE). Photo: M. H. Grayum. —31 (bottom L). *P. rothschuhianum*, showing strands of pollen emerging from anthers (*Croat 35657*). —32 (bottom R). Insect visitors to newly opening spadix of *P. anisotomum*. Large beetles shown (*Erioscelis colombica*) are legitimate pollinators; smaller insects (*Veella*, order *Hemiptera*) are frequent visitors to *Philodendron* but play no known role in their biology. Photo: H. Young.

Figures 33–36. —33 (top L). *Philodendron hebetatum*, showing spathe beginning to break up to expose mature berries (*Croat & Monsalve 61396*). —34 (top R). *P. findens*, showing scar left by fallen spathe and coarsely striate peduncle apex (*Croat 38218*). —35 (bottom L). *P. pseudauriculatum*, showing mature infructescences with spathe and staminate portion of spadix fallen (*Croat & Zhu 76251*). —36 (bottom R). *P. brenesii*, showing infructescence with exfoliating spathe and partially consumed berries (*Croat 35519*).

Figures 37–40. *Philodendron advena*. —37 (top L). (*Croat & Hannon 63107*) Adult blade. —38 (top R). (*Croat & Hannon 65549*) Stem with two pre-anthesis inflorescences and semipersistent cataphylls and an elongated petiole sheath. —39 (bottom L). (*Croat & Hannon 63107*) Infructescences (one showing spathe already fallen). —40 (bottom R). (*Croat & Hannon 63430*) Infructescence nearing maturity (showing cut open view). Because of oblique attachment, adaxial side of spadix is longer than the abaxial side.

Figures 41–44. 41–43. *Philodendron albisuccus*. 41, 42 (top L & R). (*Croat 37851*). —43 (bottom L). (*Croat 68940*). —44 (bottom R). *P. anisotomum* (*Croat & Hannon 64364*).

Figures 45–48. *P. alticola* (*Croat 74906*). —45 (top L). Stem with post-anthesis inflorescence. —46 (top R). Juvenile and pre-adult leaves. —47, 48 (bottom L & R). Adult leaves.



Figures 49–52. *Philodendron angustilobum*. —49 (top L). (*Croat 61162*) Habit, in cultivation. —50 (top R). Plants displaced from trees, with inflorescences (*Croat & Hannon 64522*). 51, 52. (*Croat 61162*). —51 (bottom L). Inflorescence at anthesis. —52 (bottom R). Habit in cultivation.

Figures 53–56. *Philodendron anisotomum*. —53 (top L). Habit in cultivation (Berlin Botanical Garden (031-60-74-83)). —54 (top R). Stem with anchor roots spreading from stem. —55 (bottom L). Leaf in cultivation (*Croat & Hannon 64364*). —56 (bottom R). Plant with inflorescence in cultivation (*Selby 80-1668*, from Mexico, Chiapas, Ocosingo).

Figures 57–60. *Philodendron annulatum*. 57–59. (*Croat 74803*). —57 (top L). Habit. —58 (top R). Stem and inflorescences. —59 (bottom L). Leaf with petiole showing purple ring at apex. —60 (bottom R). (*Croat 74855*) Showing stem with cataphyll, unopened inflorescence, and bracteole.

Figures 61–64. *Philodendron antonioanum* (*Croat & Zhu 76909*). —61 (top L). Habit. —62 (top R). Leaf. —63 (bottom L). Inflorescences partially obscured by cataphylls. —64 (bottom R). Leaves, both lower and upper surfaces.

Figures 65–68. —65 (top L). *Philodendron auriculatum*, habit (cultivated by John Banta). 66–68. *P. aromaticum*. 66, 67. (*Croat 68382*). —66 (top R). Habit. —67 (bottom L). Stem and inflorescences. —68 (bottom R). (*Croat 68423*) Open inflorescence.

Figures 69–72. *Philodendron auriculatum*. —69 (top L). (*Croat 59730*) Habit in cultivation. —70 (top R). (*Croat & Grayum 35205*) Open inflorescence. 71, 72. (*Croat 32956*) (photo: P. Malesevich). —71 (bottom L). Open inflorescence showing protruded spadix. —72 (bottom R). Sharply 2-ribbed cataphyll.

Figures 73–76. —73 (top L). *Philodendron advena* (*Croat 47777*), habit. —74 (top R). *P. angustilobum*, post-anthesis inflorescences, showing spadix with spathe cut away and the discoloration of the staminate spadix (*Croat 61162*). —75 (bottom L). *P. anisotomum* (*Croat 78892*), habit. —76 (bottom R). *P. basii*, habit (cultivated by Conrad Fleming).

Figures 77–80. 77, 78. *Philodendron bakeri*. —77 (top L). Plant hand-held (*Croat 37508*). —78 (top R). Habit, showing abaxial surfaces of blades (*Croat 67456*). —79, 80 (bottom L & R). *P. breedlovei* (*Breedlove 345181*).

Figures 81–84. *Philodendron basii* (*Croat 45442*). —81 (top L). Habit (cultivated at MO; photo: P. Malesevich). 82, 83 (Cultivated at SEL). —82 (top R). Leaf, abaxial surface. —83 (bottom L). Stem with intact cataphylls and closed petiole sheaths. —84 (bottom R). Stem with inflorescence.

Figures 85–88. —85 (top L). *Philodendron breedlovei*, open inflorescence (*Breedlove 35181*) (photo: D. Breedlove). 86–88. *P. brenesii*, habit. —86 (top R). (*Croat 67578*). —87 (bottom L). (*Croat 68084*). —88 (bottom R). Apex of stem with bases of petioles, cataphyll, and unopened inflorescence (*Croat 78806*).

Figures 89–92. —89 (top L). *Philodendron brenesii*, habit (*Croat 43521*). 90, 91. *P. brevispathum* (*Croat 58586*). —90 (top R). Habit. —91 (bottom L). Stem with entire cataphyll and unopened inflorescence. —92 (bottom R). *P. brewsterense* (*De Nevers et al. 5545*).

Figures 93–96. *Philodendron brunneicaule*. 93–95. (*Croat & Zhu 76381*). —93 (top L). Habit. —94 (top R). Plant showing stem attached to small tree with anchoring roots and inflorescence arising from elongated petiole sheath (plant displaced). —95 (bottom L). Habit (plant displaced). —96 (bottom R). Inflorescence cut open (*Croat 68713*).

Figures 97–100. —97 (top L). *Philodendron brunneicaule*, leaf blade adaxial surface (*Croat & Zhu 76581*). 98–100. *P. chiriquense* (*Croat 69068*). —98 (top R). Leaf blade adaxial surface. —99 (bottom L). Stem apex showing inflorescences emerging from cataphyll fibers. —100 (bottom R). Inflorescence with tube portion cut open.

Figures 101–104. —101 (top L). *Philodendron chirripoense* (*Burger & Liesner 7139*). —102 (top R). *P. clewellii* (*Gentry & Clewell 7028*). 103, 104. *P. coloradense*. —103 (bottom L). Habit (*Croat 75039*). —104 (bottom R). Plant hand-held with inflorescences (*Croat 37168*).

Figures 105–108. 105, 106. *Philodendron coloradense*. —105 (top L). Stem with inflorescences (*Croat 37168*). —106 (top R). Habit (*Croat 75039*). —107 (bottom L). *P. chiriquense*, habit (*Croat 69068*). —108 (bottom R). *P. cotonense* (plant held by T. K. Croat) (*Croat 66262*).

Figures 109–112. *Philodendron copense*. —109 (top L). Habit (*Croat 60159*). —110 (top R). Cluster of inflorescences (one open) (*Croat 44729*). —111 (bottom L). Stem with D-shaped petioles and unopened inflorescences (*Croat 44729*). —112 (bottom R). *P. crassispathum*, habit (*Croat 48444*).

Figures 113–116. 113–115. *Philodendron copense*. —113 (top L). Leaf blade adaxial surface (*Croat 44729*). 114. 115. (*Croat 68765*). —114 (top R). Leaf blade abaxial surface. —115 (bottom L). Inflorescence emerging from cataphyll fibers. —116 (bottom R). *P. correae*, habit (*Croat & Zhu 76395*).

Figures 117–120. 117–119. *Philodendron correae* (*Croat 66748*). —117 (top L). Habit. —118 (top R). Habit with inflorescence and infructescence. —119 (bottom L). Plant with mature infructescence and fully sheathed petioles. —120 (bottom R). *P. cotobrusense* (*Grayum & Hammel 5689*).

Figures 121–124. 121–123. *Philodendron cotonense*. —121 (top L). Habit (*Croat 66169*). 122, 123. (*Croat 66504*). —122 (top R). Habit showing abaxial surfaces. —123 (bottom L). Stem with inflorescences. —124 (bottom R). *P. crassispathum*, habit (*Croat 33150*).

Figures 125–128. 125, 126. *Philodendron cretosum* (*Croat & Zhu 76661*). —125 (top L). Habit. —126 (top R). Apex of stem with persistent cataphyll fibers, obtusely sulcate petioles, and an unopened inflorescence. 127, 128. *P. crassispathum* (*Croat 33150*). —127 (bottom L). Habit. —128 (bottom R). Inflorescence with spathe tube cut open.

Figures 129–132. 129, 130. *Philodendron davidsonii* subsp. *davidsonii*, habit in cultivation. —129 (top L). (*Davidson 7097*). —130 (top R). (*Croat 522324*). 131, 132. *P. davidsonii* subsp. *bocatoranum*. —131 (bottom L). Habit in cultivation (*Croat 38177*). —132 (bottom R). Apex of stem with unopened inflorescences (*Croat 36858*).

Figures 133–136. 133–135. *Philodendron davidsonii* subsp. *bocatoranum* (*Croat 38177*). —133 (top L). Habit in cultivation. —134 (top R). Open inflorescence. —135 (bottom L). Leaf blade abaxial surface. —136 (bottom R). *P. davidsonii* subsp. *davidsonii*, open inflorescence (*Davidson 7097*).

Figures 137–140. *Philodendron dodsonii*. 137, 138. (*Croat 72982*). —137 (top L). Habit. —138 (top R). Apex of stem with petioles, cataphylls, and unopened inflorescence. —139 (bottom L). Unopened inflorescence (*Croat & Hannon 79114*). —140 (bottom R). Inflorescence on abaxial blade surface showing normal open nature.

Figures 141–144. 141–143. *Philodendron dodsonii*. 141, 142. Habit. —141 (top L). (*Croat 72982*). —142 (top R). (*Croat & Hannon 79114*). —143 (bottom L). Leaf blade abaxial surface (*Croat 72982*). —144 (bottom R). *P. cretosum*, habit (*Croat 67123*).

Figures 145–148. *Philodendron dolichophyllum*. —145 (top L). Natural habit on road bank (*Croat & Zhu 77008*). 146, 147. (*Croat 67350*). —146 (top R). Plant displaced from tree. —147 (bottom L). Apex of stem with unopened inflorescence. —148 (bottom R). Mature infructescence. Not collected. Photo from El Llano–Carí Road, Panamá Province (photo: D. Burnett).

Figures 149–152. —149 (top L). *Philodendron crassispathum*, stem with unopened inflorescence (*Croat 33150*). —150 (top R). *P. dodsonii*, habit with inflorescences arising from elongated petiole sheaths (*Croat 72982*). —151 (bottom L). *P. dolichophyllum*, habit (*Croat 22908*). —152 (bottom R). *P. dressleri*, leaf blade abaxial surface (*Croat 45360*).

Figures 153–156. 153, 154 (top L & R). *Philodendron dominicalense* (*Croat 35268*). —155 (bottom L). *P. dwyeri* (*Dwyer & Liesner 12334*). —156 (bottom R). *P. edenudatum*, habit (*Croat & Zhu 77157*).

Figures 157–160. *Philodendron dressleri*. 157, 158. (*Croat 45360*). —157 (top L). Habit. —158 (top R). Stem with unopened inflorescences. 159, 160. Cultivated at Joseph Fondeur's. —159 (bottom L). Habit. —160 (bottom R). Apex of stem showing persistent, intact cataphyll at uppermost node and petiole bases with closed sheath.

Figures 161–164. *Philodendron edenudatum*. 161, 162. (*Croat & Zhu 77087*). —161 (top L). Leaf blade adaxial surface. —162 (top R). Stem apex. 163, 164. (*Croat 33988*). —163 (bottom L). Blade abaxial surface, showing purplish spots on petiole and lower midrib (photo: P. Malesevich). —164 (bottom R). Inflorescence in cultivation in final stages of closure.

Figures 165–168. *Philodendron ferrugineum.* —165 (top L). Habit (*Croat 33732*). —166 (top R). Habit (*Croat 75155*). —167 (bottom L). Cluster of inflorescences (*Croat & Zhu 77029*), juvenile foliage. —168 (bottom R). Juvenile foliage (*Croat 75116*).

Figures 169–172. 169–171. *Philodendron findens*. —169 (top L). Showing young blade before shredding occurs (*Croat 67153*). —170 (top R). Showing divided blades which naturally become pinnate (*Croat 67919*). —171 (bottom L). Showing winged petiole (*Croat & Zhu 76502*). —172 (bottom R). *P. folsomii* (*McPherson 13619*).

Figures 173–176. 173, 174. *Philodendron ferrugineum*. —173 (top L). Habit (*Croat 34349*). 174, 175. Cluster of inflorescences with one open. —174 (top R). (*Croat 25098*). —175 (bottom L). *P. findens* (*Croat 38218*). —176 (bottom R). *P. folsomii* (*McPherson 13619*).

Figures 177–180. 177, 178. *Philodendron findens* (*Croat 38218*). —177 (top L). Apex of stem with unopened inflorescences. —178 (top R). Open inflorescence. —179 (bottom L). *P. fortunense*, habit (*Croat 67921*). —180 (bottom R). *P. glanduliferum*, habit with open inflorescence (hand-held) (*Croat 39753*).

Figures 181–184. *Philodendron fortunense*. —181 (top L). Habit (hand-held by author) (*Croat 50000*). —182 (top R). Habit (*Croat 66714*). —183 (bottom L). Leaf showing abaxial surface and winged petiole (*Croat 48727*). —184 (bottom R). Stem apex with cluster of immature inflorescences (*Croat 66714*).

Figures 185–188. —185 (top L). *Philodendron ferrugineum*, cluster of inflorescences with one cut open (*Croat 25098*). 186–188. *P. fragrantissimum*. 186, 187 (top R & bottom L). (*Granville 5975*) Cultivated at the University of Utrecht Botanical Garden. —188 (bottom R). Habit with leaves with D-shaped petioles and inflorescences emerging from cataphylls (*Croat 11526*).

Figures 189–192. 189–191. *Philodendron fragrantissimum*. —189 (top L). Habit (*Croat 11526*). —190 (top R). Apex of stem with persistent cataphyll fibers (*Croat 53912*). —191 (bottom L). Juvenile leaves (*Croat 9003*). —192 (bottom R). *P. gigas*, stem with petiole bases and intact cataphyll fibers (*Croat 33680*).

Figures 193–196. *Philodendron gigas* (*Croat & Zhu 76988*). —193 (top L). Plant on ground with loose inflorescences. —194 (top R). Plant held by author. —195, 196 (bottom L. & R). Loose inflorescences showing unopened spathe and prophylls.

Figures 197–200. *Philodendron glandulíferum*. 197–199. *P. glandulíferum* subsp. *camilloanum*. 197, 198 (top L & R). Cultivated by Roberto Burle-Marx. —199 (bottom L). Open inflorescence (*Croat 62069*) (Venezuela). —200 (bottom R). *P. glandulíferum* subsp. *glandulíferum*. Cultivated at the Munich Botanical Garden (coll. (*Förther s.n.*), San Jose, Guatemala).

Figures 201–204. 201, 202. *Philodendron glanduliferum* var. *glanduliferum*. —201 (top L). (*Croat 43909*) Leaves showing petiolar glands. —202 (top R). Showing weathered cataphyll fibers (*Croat 39753*). 203, 204. *P. grandipes*. — 203 (bottom L). Habit (displaced) (*Croat & Watt 70200*). —204 (bottom R). Apex of stem with intact cataphylls and unopened inflorescences (*Croat 61323*) (Colombia. Valle: Bajo Calima).

Figures 205–208. —205 (top L). *Philodendron gigas*, blade adaxial surface with unopened inflorescence (*Croat & Zhu 76988*). —206 (top R). *P. grandipes*, open inflorescence (*Croat 33648*) (photo: P. Malesevich). —207, 208 (bottom L & R). *P. granulare* (*Croat & Porter 15543*).

Figures 209–212. *Philodendron grayumii*. —209 (top L). Leaf blade adaxial surface (*Croat 66814*). —210 (top R). Cluster of unopened inflorescences (*Croat & Zhu 76524*). —211 (bottom L). Blade adaxial surfaces (*Croat 66969*). —212 (bottom R). Apex of stem with open inflorescence; petiole with obtusely sulcate base (*Croat 74840*).

Figures 213–216. *Philodendron grayumii*. 213, 214 (*Croat 66794*). —213 (top L). Habit. —214 (top R). Open inflorescence. —215 (bottom L). (*Croat & Zhu 77202*) Habit. —216 (bottom R). *P. grandipes*. habit (*Croat & Zhu 76664*).

Figures 217–220. —217 (top L). *Philodendron hammelii* (*Hammel 3551*). 218–220. *P. hebetatum*. —218 (top R). Habit (*Croat 56715*). —219 (bottom L). Cluster of inflorescences (*Croat 73150*). —220 (bottom R). Open inflorescence in cultivation (*Croat 33773*).

Figures 221–224. *Philodenron hederaceum*. 221–223. *P. hederaceum* var. *hederaceum*. 221, 222. Habit. —221 (top L). (*Croat 70891*). —222 (top R). (*Croat 69834*). —223 (bottom L). Cultivated at Kiev Botanical Garden (juvenile form with velvety leaves). —224 (bottom R). *P. hederaceum* var. *kirkbridei*, close-up of stem showing minutely warty surface and anchor roots (*Croat 75108*).

Figures 225–228. 225, 226. *Philodendron hebetatum*. —225 (top L). Leaf blade adaxial surface (*Croat 73150*). —226 (top R). Open inflorescence (*Croat 69231*). 227, 228. *P. heleniae* (*Croat & Zhu 76738*). —227 (bottom L). Habit. —228 (bottom R). Habit with inflorescences (displaced from tree).

Figures 229–232. 229, 230. *Philodendron heleniae*. —229 (top L). Cluster of inflorescences (one open) (*Croat & Zhu 76738*). —230 (top R). Open inflorescence with protruding spadix (*Croat 61275*) (Colombia. Valle: Bajo Calima). 231, 232. *P. jacquinii*. —231 (bottom L). Habit (*Croat 69835*). —232 (bottom R). Habit with inflorescences (*Croat 12458*).

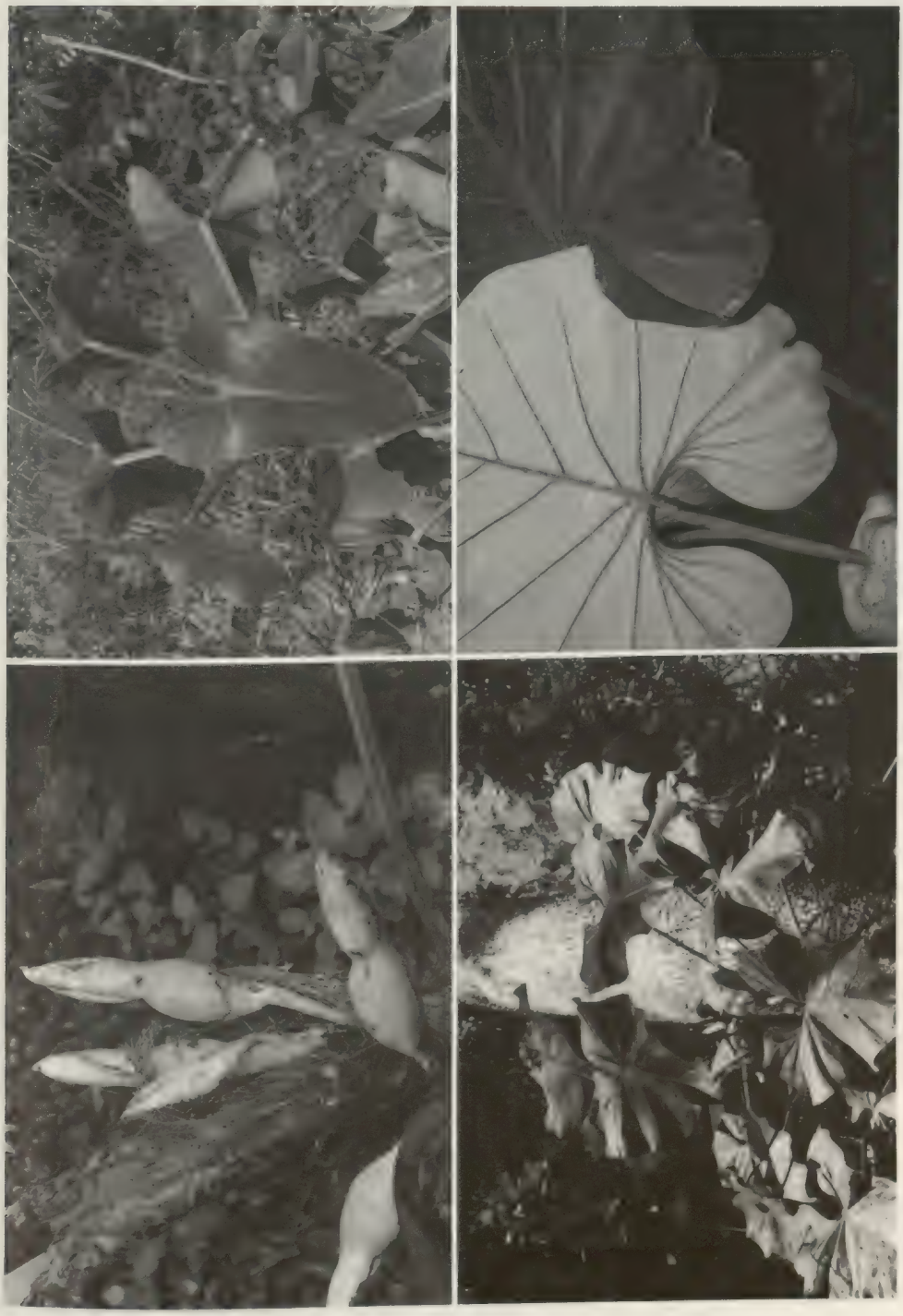
Figures 233–236. *Philodendron immixtum*. —233 (top L). Habit (hand-held) (*Croat 10283*). —234 (top R). Habit (*Croat 34592*). 235. 236. (*Croat 33574*). —235 (bottom L). Habit in cultivation. —236 (bottom R). Open inflorescence.

Figures 237–240. —237 (top L). *Philodendron jacquinii*, showing infructescences with fallen spathe (*Croat 14911*). —238, 239 (top R & bottom L). *P. jefense* (*McPherson 10038*). —240 (bottom R). *P. knappiae*, habit (*Croat 67982*).

Figures 241–244. 241, 242. *Philodendron jacquinii*. —241 (top L). Blade adaxial surface (*Croat & Zhu 77072*). —242 (top R). Inflorescences cut open showing prolonged styles (*Croat 12458*). —243 (bottom L). *P. jodavisianum*, habit (*Croat 60080*). —244 (bottom R). *P. knappiae*, blade adaxial surface (*Croat 67982*).

Figures 245–248. *Philodendron jourisianum*. —245 (top L). Cataphyll fibers (*Croat 60080*). —246 (top R). Blade adaxial surface (*Gravum 3216*). —247 (bottom L). Habit (*Croat 60450*). —248 (bottom R). Open inflorescence (*Croat 67213*).

Figures 249–252. —249 (top L). *Philodendron knappiae*, habit (*Croat 67982*). 250–252. *P. lazorii* Croat. 250, 251. (*Croat 68953*). —250 (top R). Leaf blade adaxial surface. —251 (bottom L). Stem apex with cataphyll fibers and closed inflorescences. —252 (bottom R). (*Croat 69833*) Stem with cluster of inflorescences and persistent intact cataphylls.



Figures 253–256. —253 (top L). *Philodendron jedanisianum*, stem apex with persistent cataphyll fibers and cluster of inflorescences (*Croat 67129*). —254 (top R). *P. knappiae*, habit (*Croat 67982*). 255, 256. *P. lazorii*. —255 (bottom L). Habit (*Croat 69833*). —256 (bottom R). Leaf blades showing adaxial and abaxial surfaces (*Croat & Zhu 77126*).

Figures 257–260. 257, 258. *Philodendron lazorii*. —257 (top L). Leaf blade adaxial surfaces (*Croat & Zhu 77126*). —258 (top R). Stem apex with partially intact cataphyll fibers (*Croat 69833*). 259, 260. *P. lentii*. —259 (bottom L). Habit, displaced from tree (*Croat 50041*). —260 (bottom R). Stem with open inflorescence (*Croat 66647*).

Figures 261–264. *Philodendron lentii*. —261 (top L). Habit (*Croat 66647*). 262, 263. (*Croat 67538*). —262 (top R). Leaves showing abaxial surfaces and D-shaped petioles. —263 (bottom L). Habit. —264 (bottom R). Showing stem with sulcate petiole base (*Croat 66391*).

Figures 265–268. —265 (top L). *Philodendron lentii*, habit (*Croat 67163*). 266, 267. *P. ligulatum* var. *ligulatum* (*Croat 49195*). —266 (top R). Habit. —267 (bottom L). Inflorescence with protruding spadix. —268 (bottom R). *P. llanense*, open inflorescence with protruding spadix and cut-open spathe tube (*Mori 4628*).

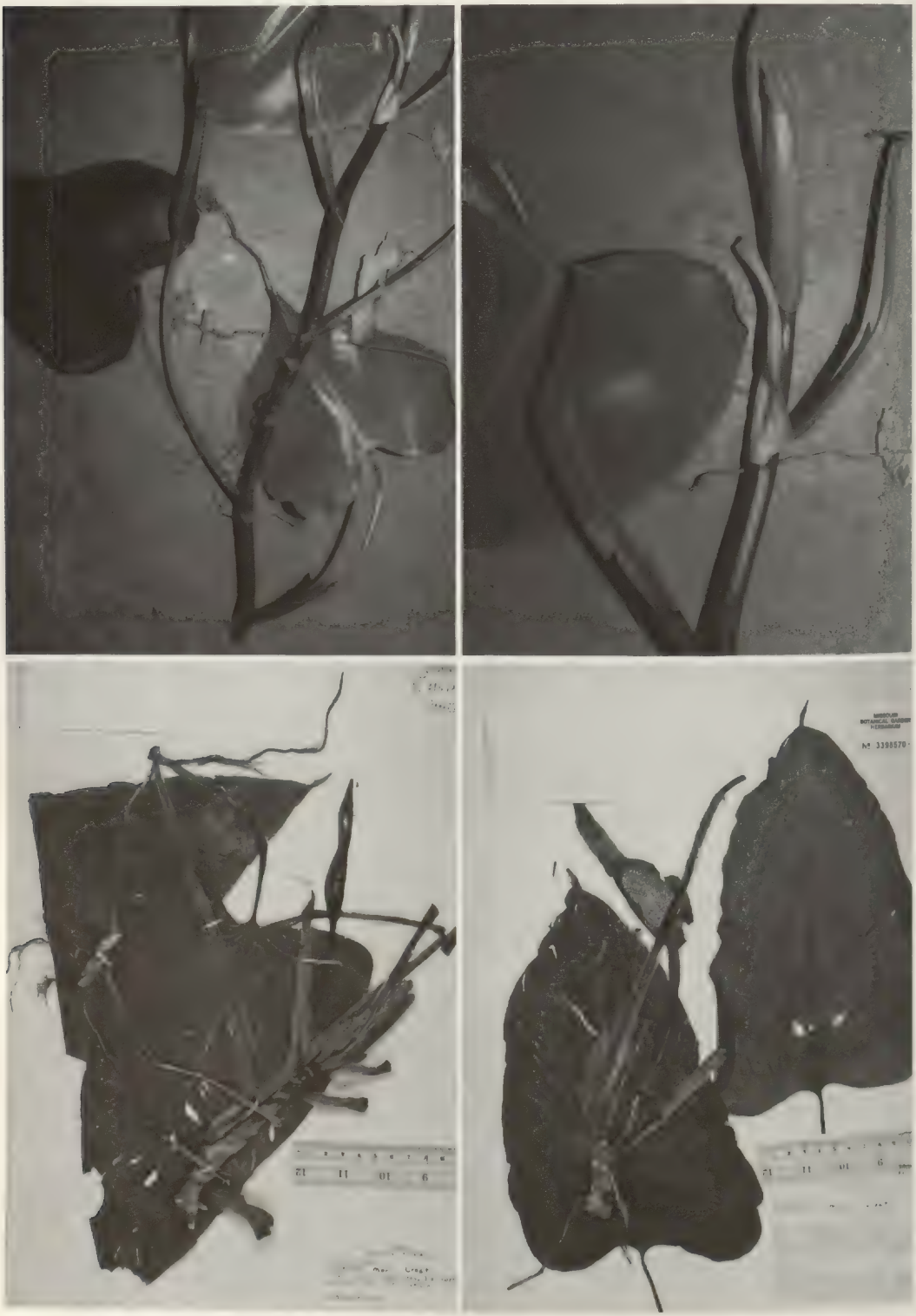
Figures 269–272. 269–271. *Philodendron ligulatum* var. *ligulatum*. —269 (top L). Habit (*Croat 67318*). —270 (top R). Stem with open inflorescence (*Croat 34302*). —271 (bottom L). Habit (plant displaced from tree) (*Croat & Zhu 76954*); note dark ring separating petiole from blade. —272 (bottom R). *P. ligulatum* var. *ovatum*, habit (*Croat & Zhu 76754*).

Figures 273–276. —273 (top L). *Philodendron ligulatum* var. *ovatum*, habit (*Croat & Zhu 76888*). 274–276. *P. ligulatum* var. *heraclioanum* (*Croat & Zhu 77098*). —274 (top R). Habit showing blades spotted on lower surface. —275 (bottom L). Leaf blade adaxial surface showing sharply D-shaped petiole with narrow wing and dark ring at petiole apex. —276 (bottom R). Unopened inflorescence, stem, and D-shaped petiole.

Figures 277–280. 277, 278. *Philodendron llanense*. —277 (top L). Leaf blade adaxial surface (*Croat 60505*). —278 (top R). Cluster of unopened inflorescences (*Croat & Zhu 76993A*). —279, 280 (bottom L & R). *P. madronense* (*Hammel & McPherson 14526*).

Figures 281–284. *Philodendron malesevichiae* (*Croat 74818*). —281 (top L). Habit. —282 (top R). Stem with intact, persistent cataphylls. —283 (bottom L). Petiole with conspicuous, trichome-like glands. —284 (bottom R). Open inflorescence.

Figures 285–288. *Philodendron mexicanum*. 285, 286. (*Croat & Bay 65778*). —285 (top L). Habit, displaced from tree. —286 (top R). Stem close up. 287, 288. Cultivated by Monroe Birdsey (photo: K. Upton). —287 (bottom L). Inflorescence. —288 (bottom R). Open spathe.



Figures 289–292. 289, 290. *Philodendron microstictum* (*Croat & Hannon 79210*). —289 (top L). Stem, leaf blades, inflorescence. —290 (top R). Cataphyll, anchor roots. 291, 292. *P. morii*. —291 (bottom L). (*Liesner 567*). —292 (bottom R). (*Hammel & McPherson 14530*).

Figures 293–296. *Philodendron niqueanum*. 293–295. (*Croat 37942*). 293, 294 (top L & R). Adult leaves. —295 (bottom L). Juvenile leaves. —296 (bottom R). Juvenile leaves in cultivation (*Croat 37886*) (photo: P. Malesevich).

Figures 297–300. 297–299. *Philodendron panamense* (*Croat 55184*). —297 (top L). Leaf blade adaxial surface. —298, 299 (top R & bottom L). Open inflorescences and sharply 2-low-ribbed cataphylls. —300 (bottom R). *P. pseudauriculatum*, habit (*Croat 37595*).

Figures 301–304. *Philodendron pirrense*. 301, 302. (*Croat 37944*). —301 (top L). Adult leaf. —302 (top R). Stem with detached fibrous cataphyll and inflorescence. 303, 304. (*Croat 68952*). —303 (bottom L). Apical half of blade with loose inflorescences. —304 (bottom R). Basal half of blade.

Figures 305–308. —305 (top L). *Philodendron pirrense*, habit (*Croat 68952*). 306–308. *P. platypetiolatum*. —306 (top R). Habit, displaced from tree (*Croat 68136*). 307, 308. (*Croat 68205*). —307 (bottom L). Habit, displaced from tree. —308 (bottom R). Plant with opened inflorescence (*Croat 78878*).

Figures 309–312. 309, 310. *Philodendron pseudauriculatum* (*Croat 33526*). —309 (top L). Habit. —310 (top R). Close-up of stem with petiole bases (photo: P. Malesevich). 311, 312. *P. pterotum*. —311 (bottom L). Habit (*Croat 6581*). —312 (bottom R). Apex of stems with cluster of inflorescences and persistent cataphylls (*Croat 10792*) (cultivated at Summit Gardens).

Figures 313–316. 313, 314. *Philodendron pseudauriculatum*. —313 (top L). Habit in cultivation with leaves, inflorescence, and sharply 2-ribbed cataphylls (*Croat 33526*). —314 (top R). (*Croat 48696A*). 315, 316. *P. pterotum*. —315 (bottom L). Habit (*Croat 6581*). —316 (bottom R). Open inflorescence (*Croat 10265*).

Figures 317–320. *Philodendron purpureoviride*. 317, 318. (*Croat 59857*). —317 (top L). Leaf blade adaxial surface. —318 (top R). Habit. —319 (bottom L). Opened inflorescence. Cultivated at Wilson Botanical Garden (photo: D. Beath). —320 (bottom R). (*Croat & Zhu 76677*) Habit with cataphyll recurling and beginning to recurl.

Figures 321–324. 321–323. *Philodendron purulhense*. —321 (top L). Habit (*Croat 41752*). —322 (top R). Leaf blade adaxial surface (*Croat & Hannon 63765*). —323 (bottom L). Stem apex with unopened inflorescence (*Croat 41189*). —324 (bottom R). *P. radiatum*, cultivated at Wilson Tropical Gardens.

Figures 325–328. 325, 326. *Philodendron paraluthense* (*Croat & Hannon 63765*). —325 (top L). Leaf blade adaxial surface. —326 (top R). Plant hand-held. 327, 328. *P. radiatum* var. *pseudoradiatum* (*Croat & Hannon 63381*). —327 (bottom L). Habit. —328 (bottom R). Plant on ground with inflorescence cut open.

Figures 329–332. 329, 330. *Philodendron radiatum* var. *pseudoradiatum* (*Croat & Hannon 63381*). —329 (top L). Closed inflorescence. —330 (top R). Leaf blade on ground with a displaced post-antheis spadix. 331, 332. *P. radiatum* var. *radiatum*. —331 (bottom L). Habit (*Croat 32767*). —332 (bottom R). Pre-adult leaf blades (*Croat 66075*) (photo: P. Malesevich).

Figures 333–336. 333–335. *Philodendron radiatum* var. *radiatum*. —333 (top L). (*Croat 66816*). —334 (top R). Cultivated at the Missouri Botanical Garden trailer house in Curundu. —335 (bottom L). Habit (one leaf displaced, showing adaxial surface) (*Croat 6060*). —336 (bottom R). *P. rothschuhianum* (*Croat 74931*).

Figures 337–340. *Philodendron rothschuhianum*. —337 (top L). Adult leaves. Tortuguero National Park (not collected; photo: M. H. Grayum). —338 (top R). (*Croat & Zhu 77224*) Juvenile leaves. —339 (bottom L). Habit in cultivation at the Missouri Botanical Garden (*Croat 35657*). —340 (bottom R). Stem with inflorescences (*Croat 27704*).

Figures 341–344. *Philodendron roseospathum* var. *roseospathum*. —341 (top L). Habit in cultivation showing leaves and intact cataphylls (*Croat 35931*). 342–344. (*Croat 57515*). —342 (top R). Habit. —343 (bottom L). Stem with intact cataphylls and inflorescences. —344 (bottom R). Open inflorescence.

Figures 345–348. —345 (top L). *Philodendron roseospathum*, cultivated at Selby Gardens (SEL-92-353; photo: V. Sawyer). —346 (top R). *P. sagittifolium*, habit (*Croat 67697*). 347, 348. *P. rothschuhianum*. —347 (bottom L). Habit (*Croat 74931*). —348 (bottom R). Stem with cluster of inflorescences at apex of stem (*Croat & Grayum 60276*).

Figures 349–352. —349 (top L). *Philodendron roseospathum* var. *angustilaminatum* (*Hammel 3133*). 350–352. *P. sagittifolium*. —350 (top R). Leaf blade adaxial surface (*Croat 67918*). —351 (bottom L). Apex of stem with petiole bases, cataphylls, and inflorescences (*Croat & Grayum 60259*). —352 (bottom R). Open inflorescence (*Croat 69731*).

Figures 353–356. *Philodendron sagittifolium*. —353 (top L). Leaf blade adaxial surface (*Croat 74939*). —354 (top R). Plant with open inflorescence (*Croat 33179*). —355 (bottom L). Inflorescence with open spathe and protruding spadix (*Croat 69731*). —356 (bottom R). Leaf blade adaxial surface (*Croat 60506*).

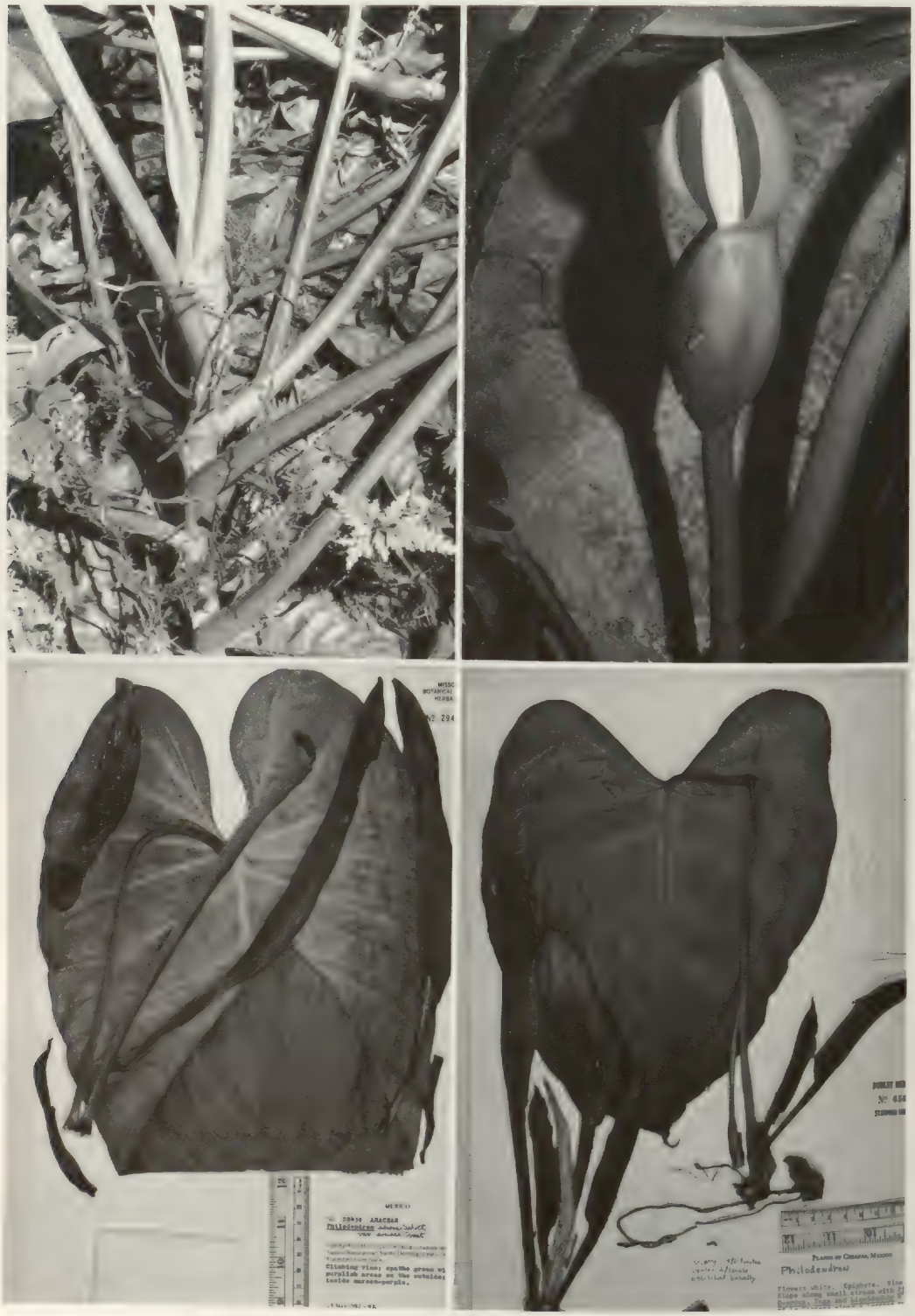
Figures 357–360. *Philodendron scalarinerve*. —357 (top L). Habit, plant displaced on ground (*Croat 67203*). —358 (top R). Stem apex with petiole bases and persistent cataphyll fibers (*Croat 68723*). —359 (bottom L). Plant with inflorescence, displaced on ground (*Croat 66959*). —360 (bottom R). Open inflorescence (*Croat 67203*).

Figures 361–364. 361–363. *Philodendron scalarinerve*. —361 (top L). Habit (*Croat & Zhu 76419*). —362 (top R). Habit (*Croat 68722*). —363 (bottom L). Cluster of inflorescences (*Croat 68692*). —364 (bottom R). *P. smithii* Engl., displaced leaf blade with pre-anthesis and slightly post-anthesis inflorescences (*Croat 45046*).

Figures 365–368. *Philodendron schottianum*. —365 (top L). Leaf blade adaxial surface (*Croat 74991*). 366–368. (*Croat & Zhu 76518*). —366 (top R). Leaf blade adaxial surfaces. —367 (bottom L). Stem apex with partially intact cataphyll fibers and a cluster of inflorescences. —368 (bottom R). Cluster of inflorescences (one partially open).

Figures 369–372. 369–371. *Philodendron schottianum*. —369 (top L). Leaf blade adaxial surface (*Croat 66505*). —370 (top R). Stem apex with partially decomposed cataphyll fibers and immature inflorescences (*Croat 74991*). —371 (bottom L). Open inflorescence emerging from persistent cataphyll fibers (*Croat 35620*). —372 (bottom R). *P. smithii*, blade adaxial surfaces (*Croat & Hannon 64588*).

Figures 373–376. —373 (top L). *Philodendron smithii*, habit (*Croat & Hannon 64524*). —374 (top R). *P. squamicaule*, habit (*Croat & Zhu 76798*). —375 (bottom L). *P. squamipetiolatum*, juvenile plant (*Croat 74857*). —376 (bottom R). *P. straminicaule*, habit (*Croat 69013*).



Figures 377–380. 377, 378. *Philodendron smithii*. —377 (top L). Stem apex, displaced on ground (*Croat & Hannon 64588*). —378 (top R). Open inflorescence (*Croat 40079*). 379, 380. *P. sousae*. —379 (bottom L). (*Davidse et. al. 20450*). —380 (bottom R). (*Breedlove 25142*).

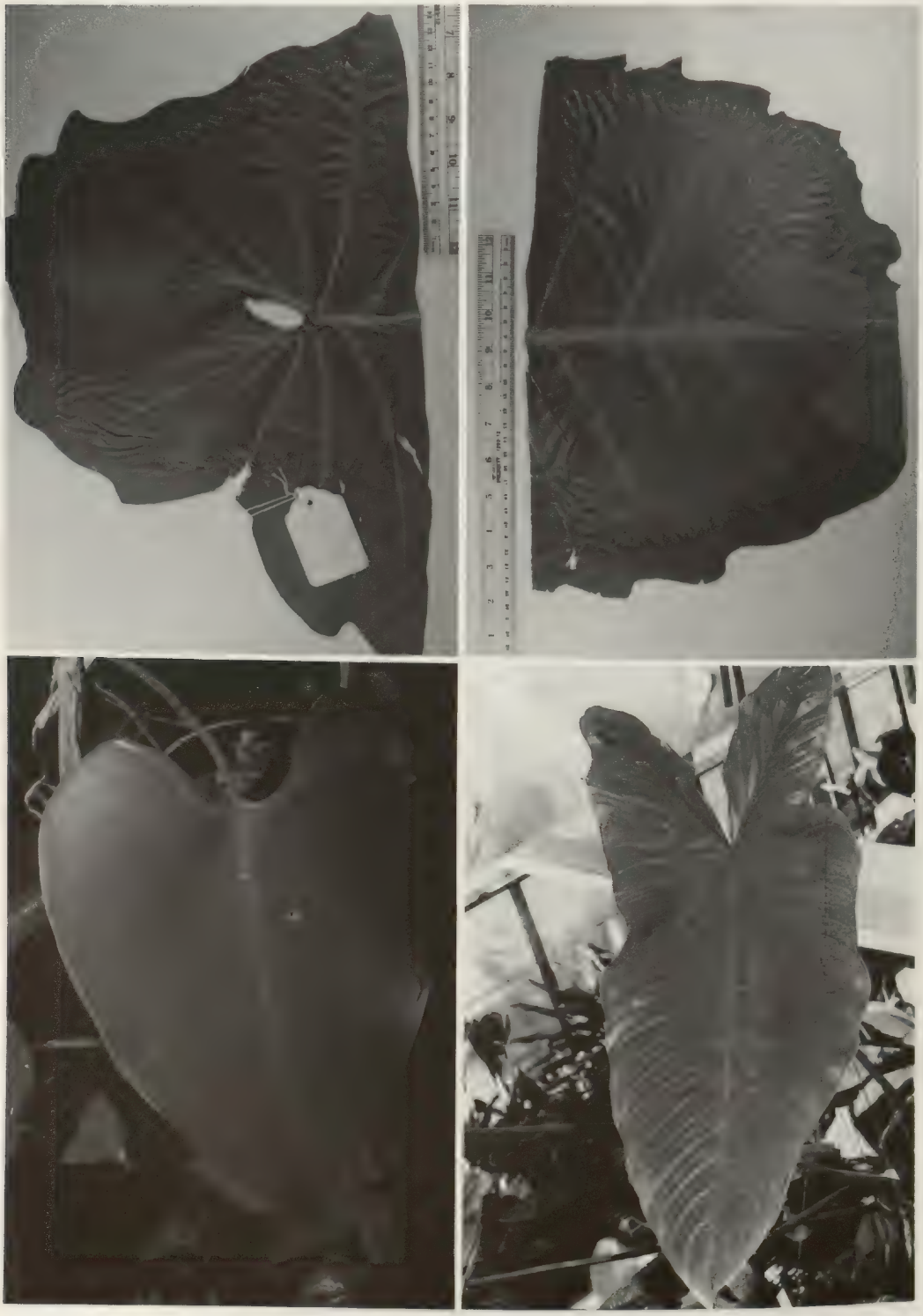
Figures 381–384. *Philodendron squamicaule* (*Croat & Zhu 76798*). —381 (top L). Leaf blade adaxial surfaces. —382, 383 (top R & bottom L). Plant with clusters of inflorescences and persistent cataphyll fibers, displaced from original site on steep road bank. —384 (bottom R). Cluster of inflorescences, one open.

Figures 385–388. *Philodendron squamipetiolatum*. 385–387. (*Croat 74857*). —385 (top L). Habit. —386 (top R). Leaf blade adaxial surfaces. —387 (bottom L). Stem with scaly petioles. —388 (bottom R). Stem with leaf and inflorescence (*Croat 68767*).

Figures 389–392. *Philodendron straminicaule*. —389 (top L). Habit (*Croat 67920*). —390, 391 (top R & bottom L). (*Croat 69013*) Open inflorescences. —392 (bottom R). Habit (*Croat 66584*).

Figures 393–396. 393–395. *Philodendron strictum* (*Croat 59130*). —393 (top L). Leaf blade adaxial surface. —394 (top R). Plant with internodes broader than long, persistent, intact cataphylls and inflorescences, one open. —395 (bottom L). Open inflorescence. —396 (bottom R). *P. subincisum*, flowering plant in cultivation, Cornell University (*Moore & Bunting 8956*) (photo: G. S. Bunting).

Figures 397–400. 397, 398. *Philodendron striatum* (*Croat & Zhu 76311*). —397 (top L). Habit. —398 (top R). Stem apex with cataphylls with thin, intact epidermis and cluster of inflorescences. 399, 400. *P. sulcicaule*. —399 (bottom L). Plant showing ribbed stem (*Croat & Grayum 60249*). —400 (bottom R). Habit (*Croat 75167*).



Figures 401–404. 401, 402 (top L & R). *Philodendron subincisum* (*Moore & Bunting 8956*). —403 (bottom L). *P. sulcicaule*, leaf blade adaxial surface (*Croat 75167*). —404 (bottom R). *P. tenue*, leaf blade adaxial surface (*Neill 3608*).

Figures 405–408. *Philodendron tenue*. —405 (top L). Stem apex with cluster of inflorescences, one open (*Neill 3608*). 406, 407. (*Croat & Watt 70365*). —406 (top R). Habit. —407 (bottom L). Stem apex showing cataphyll fibers and unopened inflorescence. —408 (bottom R). *P. thalassicum*, abaxial leaf blade surface (*Croat 66401*).

Figures 409–412. 409, 410. *Philodendron thalassicum*. —409 (top L). Stem apex with cataphyll fibers and clusters of inflorescences (*Croat 66401*). —410 (top R). Leaf blade abaxial surface (*Croat 61191*). 411, 412. *P. tripartitum*. —411 (bottom L). Adult leaf blade adaxial surface and juvenile blades (*Croat 8605*). —412 (bottom R). Adult blades (*Croat 56108*).

Figures 413–416. 413, 414. *Philodendron tenue* (*Croat 74634*) (Venezuela. Zulia: La Fria). —413 (top L). Leaf blade adaxial surface. —414 (top R). Stem apex with cataphyll fibers and inflorescences. —415 (bottom L). *P. thalassicum*, leaf (*Croat 79049*). —416 (bottom R). *P. tripartitum*, habit (*Croat 43438*).

Figures 417–420. *Philodendron tripartitum*. 417, 418. (*Croat 71903*) Cultivated at Waimea Arboretum. —417 (top L). Habit. —418 (top R). Open inflorescence. —419 (bottom L). Leaf blade adaxial surfaces (*Croat 70136*). —420 (bottom R). Leaf blade adaxial surfaces (*Croat 56149*).

Figures 421–424. *Philodendron tripartitum*. —421 (top L). Cultivated at the Lyon Arboretum (#80-890), habit. —422 (top R). Leaf blade abaxial surface (*Croat 70136*). —423 (bottom L). Stem with open spathe (*Croat 59160*). —424 (bottom R). Habit (*Croat 56108*).

Figures 425–428. *Philodendron tysonii*. —425 (top L). Habit (*Croat 68688*). —426 (top R). Leaf blade adaxial surfaces (*Croat 67844*). —427 (bottom L). Leaf blade adaxial surfaces (*Croat 66711*) —428 (bottom R). Stem apex with cluster of inflorescences, one spathe open (*Croat & Zhu 76346*).

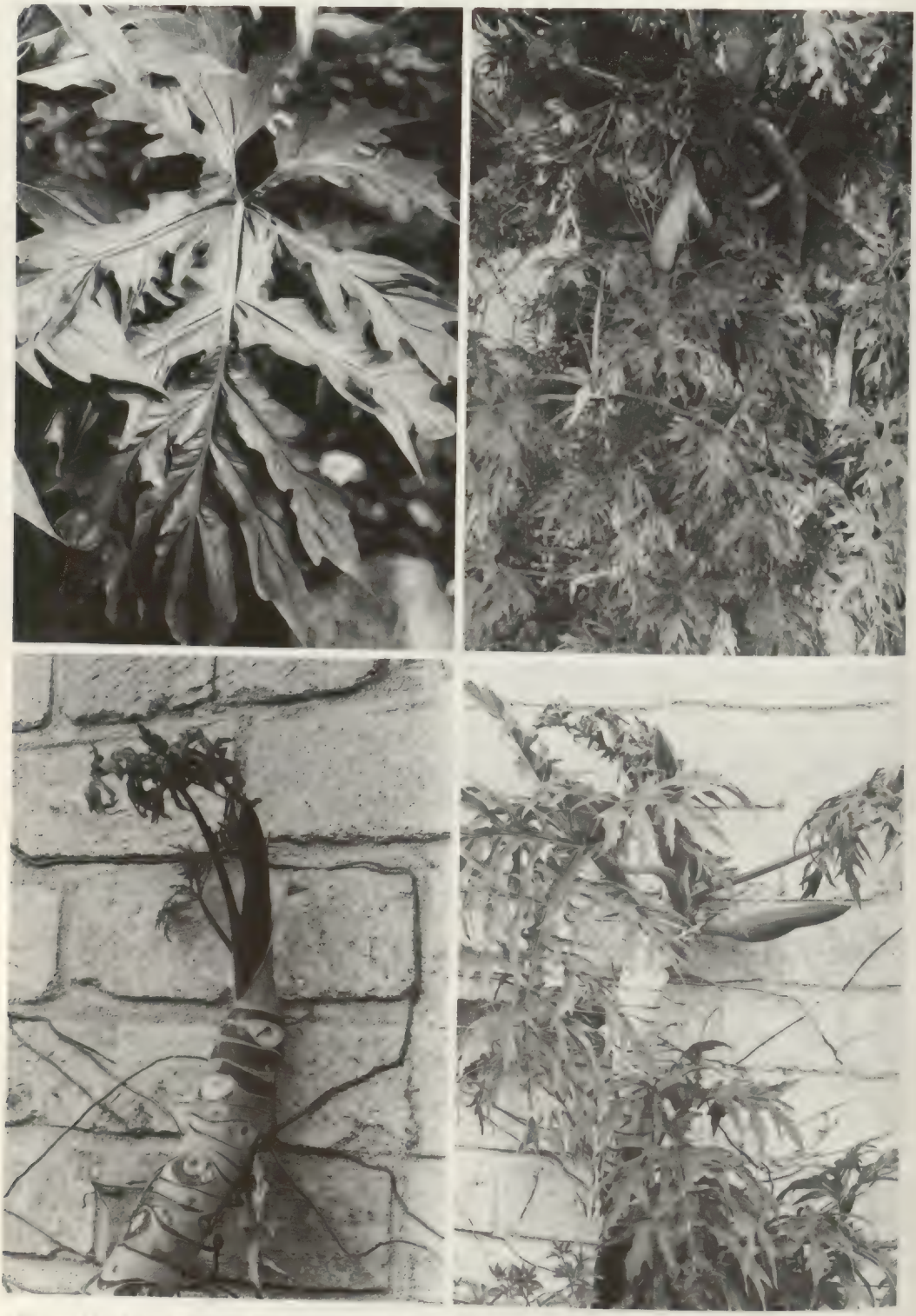
Figures 429–432. 429, 430. *Philodendron tysonii*. —429 (top L). Leaf blade surfaces (*Croat 66589*). —430 (top R). Inflorescences emerging from cataphyll fibers (*Croat 67577*). —431, 432 (bottom L & R). *P. utleyanum* (*Wilbur et al. 15068*).

Figures 425–428. *Philodendron tysonii*. —425 (top L). Habit (*Croat 68688*). —426 (top R). Leaf blade adaxial surfaces (*Croat 67844*). —427 (bottom L). Leaf blade adaxial surfaces (*Croat 66711*) —428 (bottom R). Stem apex with cluster of inflorescences, one spathe open (*Croat & Zhu 76346*).

Figures 429–432. 429, 430. *Philodendron tysonii*. —429 (top L). Leaf blade surfaces (*Croat 66589*). —430 (top R). Inflorescences emerging from cataphyll fibers (*Croat 67577*). —431, 432 (bottom L & R). *P. utleyanum* (*Wilbur et al. 15068*).

Figures 433–436. 433–435. *Philodendron verapazense*. —433 (top L). (*Carlson 1846*). —434, 435 (top R & bottom L). (*Croat 41656*). —436 (bottom R). *P. ubigantupense* (*Herrera 294*).

Figures 437–440. *Philodendron verrucosum*. —437 (top L). Habit. Panama. Panamá: Fortuna Road (not collected). —438 (top R). Leaf showing abaxial surface and petiolar scales. Costa Rica. Heredia: Braulio Carrilo Park (not collected). —439 (bottom L). Leaf showing abaxial surface with variegated coloration (*Croat 71413*). —440 (bottom R). Stem with inflorescences (*Croat 66558*).



Figures 441–444. *Philodendron warszewiczii*. 441, 442. (*Croat 40714*). —441 (top L). Leaf blade adaxial surface. —442 (top R). Habit. 443, 444. (*Croat 34814*) Cultivated at Escuela Agricola Panamericana, Zamorano, Honduras. —443 (bottom L). Plant with young leaves at beginning of rainy season; stem shows short, thick internodes and deciduous cataphylls. —444 (bottom R). Same plant with full-sized leaves and inflorescences in the middle of rainy season.

Figures 445–448. —445 (top L). *Philodendron verrucosum*, habit (*Croat 66558*). 446–448. *P. warszewiczii*. —446 (top R). Habit, cultivated by L. Garner, Homestead, Florida. —447 (bottom L). Habit (*Croat 40714*). —448 (bottom R). Stem with inflorescences (*Croat & Hannon 64136*).

Figures 449–452. —449 (top L). *Philodendron warszewiczii*, unopened inflorescences (*Croat & Hannon 64136*). 450, 451. *P. wendlandii*. Costa Rica. —450 (top R). Habit. Heredia: La Selva (not collected). —451 (bottom L). Plant with open inflorescences and sharply flattened petioles (*Croat 34141*). —452 (bottom R). *P. wilburii* var. *wilburii*, habit (*Croat 68083*).

Figures 453–456. —453 (top L). *Philodendron wendlandii*, habit (*Croat 34141*). 454–456. *P. wilburii* var. *wilburii*. —454 (top R). Habit, cultivated at the Munich Botanical Garden. —455 (bottom L). Plant displaced from tree with open inflorescences (*Croat 68083*). —456 (bottom R). Habit (*Croat 61199*).

Figures 457–460. 457, 458. *Philodendron wilburii* var. *wilburii* (*Croat 68083*). —457 (top L). Plant with closed inflorescence. —458 (top R). Open inflorescence. 459, 460. *P. wilburii* var. *longipedunculatum* (*Croat & Zhu 77083*). —459 (bottom L). Habit. —460 (bottom R). Stem displaced with closed inflorescence.

Figures 461–464. *Philodendron wilburii* var. *longipedunculatum*. —461 (top L). Blade adaxial surface (*Croat 66565*). —462 (top R). Habit (*Croat & Grayum 59879*). 463, 464. (*Croat & Grayum 60372*). —463 (bottom L). Habit. —464 (bottom R). Stem with inflorescences.

Figures 465–468. *Philodendron zhuanum* (*Croat & Zhu 76755*). —465 (top L). Habit. —466, 467 (top R & bottom L). Leaf blade adaxial surfaces. —468 (bottom R). Open inflorescence.

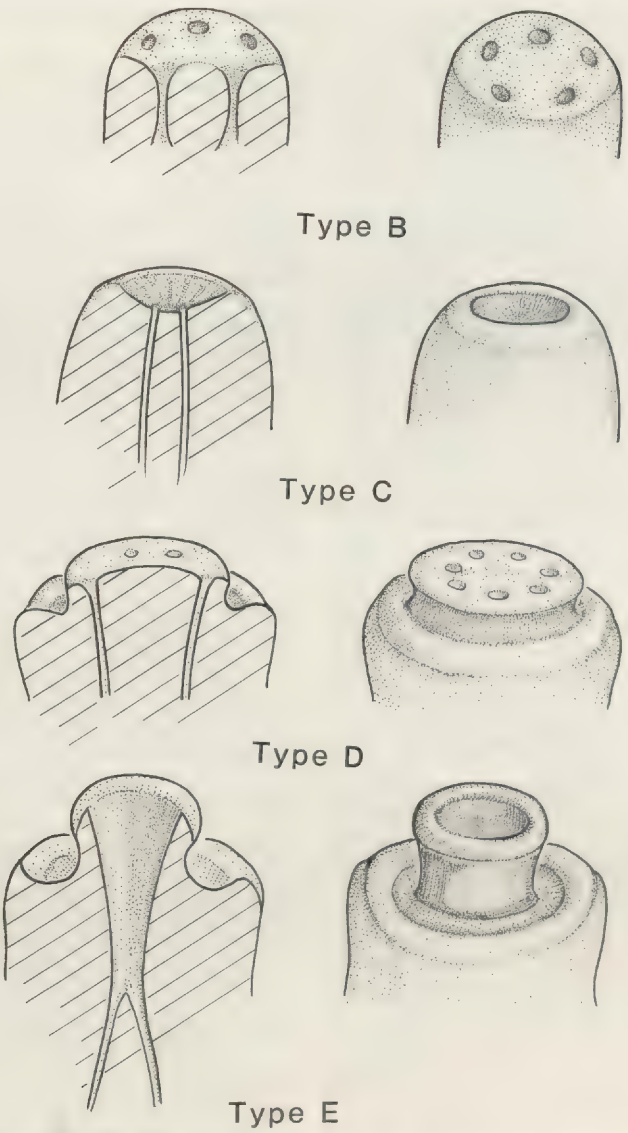


Figure 469. Style types of Central American *Philodendron* subg. *Philodendron*. Semidiagrammatic longitudinal views (left) with with cut-away views (right) showing probable route of stylar canals (based on Mayo, 1989); stigmatic area not shown. —Mayo Style Type B. *Philodendron advena*. —Mayo Style Type C. *Philodendron warszewiczii*. —Mayo Style Type D. *Philodendron ferrugineum*. —Mayo Style Type E. *Philodendron granulare*.

Index

Acorus 314
Aglaonema Schott 315, 323
Alocasia (Schott) G. Don 325
Ambrosina F. Bassi 314
Annona L. 370
Anthurium Schott 312, 315, 319, 344, 345, 346, 347, 349, 350, 369, 374, 375, 377
sect. *Pachyneurium* Croat 312
surinamense Miq. 380
Anubias Schott 323, 360
Arisaema Mart. 314
Arisarum Mill. 314
Arum L. 314
grandifolium Jacq. 380
hederaceum Jacq. 314, 458, 459, 460
lingulatum L. 314
tripartitum Jacq. 546
Asterostigma F. E. L. Fischer & C. A. Mey. 323
Baursia [without rank] 380
subg. *Eubaursia* T. Post & Kuntze 380
Bognera Nicolson 323
Bucephalandra Schott 322
Caladium Vent. 314
bauersia Rchb. 380
fragrantissimum Hook. 444
trifoliatum Densf. 546
tripartatum (Jacq.) Willd. 543
Calla L. 314
Calostigma Decne. [without rank] 324, 331
Cercestis Schott 323, 360
Colocasia Schott 314
Culcasia P. Beauv. 323, 360
Cyclanthus Poit. ex A. Rich. 374
bipartitus Poit. ex A. Rich. 370, 374
Cyclocephala 370, 508
amblyopsis Bates 361
ampliata Bates 374
conspicua Sharp 361
gravis Bates 361
kaszabi Endrödi 361
ligyrina Bates 361
mafaffa Burmeister 361
melanae Bates 361
nigerrima Bates 361, 370
rubescens Bates 361
rustica (Oliver) 361
sexpunctata Casteinau 361
Cymbopetalum Benth. 370
Dieffenbachia Schott 315, 323, 353, 360, 370, 374
longispatha Engl. 374
Dracontium L. 314, 565
Dracunculus Mill. 314
Elopium H. W. Schott 380
surinamense (Miq.) Engl. 380
Erioscelis 370
colombica Endrödi 361, 587
proba Sharp 360, 361
Euphilodendron [without rank] 324
Furtadoa M. Hotta 323, 360
Gamogyne N. E. Br. 322
Gearum N. E. Br. 323
Gorgonidium Schott 323
Gymnostachys R. Br. 314
Homalomena Schott ex Schott & Endl. 312, 322, 323, 324, 360, 370
Mangonia Schott 323
Meconostigma [without rank] 324
Microcasia Becc. 322
Monstera Adans. 324, 343, 351, 353
tuberculata Lundell var. *brevinoda* (Standl. & L. O. Williams 319, 565
Montrichardia Crueg. 323, 360
Neelia 370, 587
Nephthytis Schott 323, 360
Orontium L. 314
Peltandra Raf. 322, 323, 360
Philodendron Schott 312, 313, 314, 315, 316, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 327, 329, 336, 340, 341, 342, 343, 344, 345, 346, 347, 348, 349, 350, 351, 352, 353, 356, 357, 358, 359, 360, 361, 362, 364, 365, 366, 367, 368, 369, 370, 371, 372, 373, 374, 375, 377, 378, 379, 380, 394, 395, 436, 459, 461, 488, 546, 565, 576, 587
subg. *Euphilodendron* Engl. 317, 380
subg. *Macrolonchium* Engl. 326
subg. *Meconostigma* (Schott) Engl. 315, 317, 322, 324, 325,326, 344, 345, 346, 348, 351, 358, 360, 361, 363, 365, 367, 371,372, 373, 375, 380
subg. *Philodendron* Schott 311, 312, 314, 317, 318, 319, 320, 321, 322, 323, 324, 325, 326, 328, 338, 339, 341, 342, 343, 344, 345, 346, 347, 348, 349, 350, 351, 352, 353, 354, 356, 358, 359, 360, 361, 362, 363, 364, 366, 367, 368, 369, 370, 371, 372, 376, 377, 378, 379, 380, 382, 395, 576, 697
subg. *Pteromischum* Schott 312, 314, 315, 318, 319, 322, 324, 325, 326, 328, 343, 343, 344, 346, 351, 356, 358, 359, 360, 361, 363, 364, 367, 368, 369, 370, 373, 374, 375, 377, 380, 481
sect. *Baursia* (Rchb. ex Schott) Engl. 317, 318, 326, 327, 328, 334, 335, 338, 341, 366, 368, 576
sect. *Calostigma* (Schott) Pfeiffer 312, 317, 324, 326, 327, 328, 330, 331, 332, 335, 336, 338, 339, 347, 351, 364, 365, 366,369, 370, 392, 397, 401, 404, 405, 407, 408, 410, 414, 419, 420, 422, 424, 426, 429, 433, 435, 437, 438, 439, 442, 452, 453, 466, 468, 472, 475, 478, 480, 490, 491, 492, 493, 497, 500, 517, 526, 528, 533, 537, 538, 550, 551, 552, 553, 559, 561, 565, 575, 576
sect. *Camptogynium* K. Krause 312, 317, 318, 326, 337, 338, 576
sect. *Cardiobelium* (Schott) Engl. 351
sect. *Fruticosa* Grayum 325
sect. *Macrogynium* Engl. 312, 317, 318, 326, 332, 35, 337, 338, 347, 369, 470, 575, 576
sect. *Macrolonchium* (Schott) Engl. 317, 318, 326, 329, 337
sect. *Meconostigma* (Schott) Engl. 316, 348, 363
sect. *Oligocarpidium* Engl. 332
sect. *Oligospermium* Engl. 317, 318, 324, 326, 336, 364
sect. *Philodendron* Schott 312, 315, 316, 324, 326, 328, 330, 331, 332, 333, 335, 338, 342, 347, 351, 364, 365, 366, 370, 394, 395, 402, 409, 412, 415, 417, 418, 421, 428, 431, 441, 444, 445, 447, 448, 450, 455, 456, 459, 473, 477, 485, 488, 495, 496, 502, 503, 505, 512, 522, 524, 530, 532, 535, 540, 542, 554, 575
sect. *Philopsammos* G. S. Bunting 312, 327, 328, 338, 365, 381, 576
sect. *Platypodium* (Schott) Engl. 329

sect. *Polyspermium* Engl. .. 317, 318, 324, 326, 328, 330, 364
sect. *Polytomium* (Schott) Engl. 312, 317, 318, 326, 328, 332, 337, 338, 347, 351, 436, 507, 557, 575, 576
sect. *Pteromischum* (Schott) Engl. 315, 316, 317, 326, 327,348
sect. *Schizophyllum* (Schott) Engl. 312, 317, 318, 326, 337,338, 576
sect. *Schizoplacium* (Schott) Engl. 317, 351
sect. *Tritomophyllum* (Schott) Engl. ... 312, 317, 318, 326, 332, 335, 336, 337, 338, 347, 351, 365, 397, 398, 423, 487, 514, 549, 575, 576
subsect. *Achyropodium* (Schott) Engl. 331, 338, 448, 455, 488, 530, 532, 554, 575, 576
subsect. *Belocardium* (Schott) Engl. 332, 334
subsect. *Bulaoana* Mayo 335, 336, 337, 339, 351, 575, 576
subsect. *Canniphyllum* (Schott) Mayo 328, 331, 334, 339, 418, 428, 512, 575, 576
subsect. *Cardiobelium* (Schott) Engl. 330, 394
subsect. *Doratophyllum* 330, 338
subsect. *Eubelium* (Schott) Engl. 330
subsect. *Eucardium* (Engl.) Mayo 336, 339, 575, 576
subsect. *Glossophyllum* (Schott) Croat 327, 333, 334, 335, 339, 350, 369, 397, 406, 407, 414, 422, 424, 433, 435, 442, 452, 468, 480, 491, 492, 500, 526, 533, 538, 551, 552, 559, 561, 575, 576
subsect. *Macrobelium* (Schott) Engl. .. 332, 333, 334, 338, 339, 351, 392, 401, 404, 408, 410, 420, 426, 429, 437, 438, 439, 453, 472, 475, 478, 490, 493, 516, 529, 537, 550, 553, 565, 575, 576
subsect. *Macrolonchium* (Schott) Engl. 328, 329, 338, 445, 575, 576
subsect. *Oligocarpidium* (Engl.) Mayo 335, 339, 419, 466, 575, 576
subsect. *Philodendron* Schott 329, 330, 331, 339, 395, 402, 409, 431, 447, 450, 455, 473, 477, 485, 495, 496, 505, 522, 524, 535, 540, 542, 575, 576
subsect. *Platypetiolatum* (Schott) Engl. 338
subsect. *Platypodium* (Schott) Engl. 329, 331, 415, 421, 441, 444, 502, 575, 576
subsect. *Psoropodium* (Schott) Engl. .. 329, 330, 338, 576
subsect. *Solenosterigma* (Klotzsch ex Schott) Engl. 329, 330, 331, 335, 338, 412, 459, 503, 575, 576
ser. *Albisuccosa* Croat 331, 339, 394, 575, 576
ser. *Ecordata* Croat .. 333, 339, 369, 410, 426, 429, 478, 493, 575, 576
ser. *Fibrosa* Croat 331, 339, 395, 402, 409, 417, 431, 450, 473, 477, 485, 495, 496, 505, 522, 524, 540, 575, 576
ser. *Glossophyllum* Croat ... 334, 339, 397, 405, 407, 415, 422, 433, 442, 452, 468, 480, 492, 500, 551, 552, 559, 575, 576
ser. *Impolita* Croat 330, 333, 339, 456, 535, 542, 575, 576
ser. *Macrobelium* (Schott) Croat 333, 339, 392, 401, 404, 420, 437, 438, 439, 453, 475, 490, 497, 517, 529, 537, 553, 565, 576
ser. *Ovata* Croat 334, 335, 339, 424, 435, 491, 526, 533, 538, 561, 575, 576
ser. *Pachycaulia* Croat 333, 339, 408, 575, 576
ser. *Philodendron* Schott 330, 339, 576
ser. *Reticulata* Croat 333, 339, 472, 550, 575, 576
ser. *Velutina* Croat 330, 336, 339, 447, 575, 576
grex *Achyropodium* Schott 316, 331
grex *Baursia* Rchb. ex Schott 315, 326
grex *Belocardium* Schott 316, 332, 334
grex *Canniphyllum* Schott 315, 328
grex *Cardiobellium* Schott 316, 330
grex *Cardiophylacium* Schott 316
grex *Doratophyllum* Schott .. 316
grex *Eubelium* Schott 316, 330
grex *Glossophyllum* Schott 315, 332, 334
grex *Imbea* 316
grex *Macrobelium* Schott 316, 332, 459
grex *Macrolonchium* Schott 316, 328
grex *Meconostigma* Schott 316
grex *Oligophlebium* Schott 316, 327
grex *Platypodium* Schott 316, 329
grex *Polytomium* Schott 316
grex *Psoropodium* Schott 315, 329
grex *Pteromischum* Schott 315, 316
grex *Schizophyllum* Schott 316, 337
grex *Solenosterigma* Klotzsch 315, 329, 459
grex *Sphincterostigma* Schott 315, 316
grex *Tritomophyllum* Schott 316, 336
Gruppe *Achyropodium* Schott 317
Gruppe *Belocardium* Schott 317, 332
Gruppe *Cardiobelium* Schott 317, 330
Gruppe *Doratophyllum* Schott 335, 336, 351
Gruppe *Eucardium* Engl. 336
Gruppe *Macrobelium* Schott 317
Gruppe *Oligocarpidium* Engl. 317, 351
Gruppe *Platypodium* Schott 317
Gruppe *Solenosterigma* (Klotzsch) Schott .. 317, 335
species:
accrescens N. W. Simmonds 444
acreanum K. Krause 327
acrocardium Schott 316, 332, 461
acuminatissimum Engl. 330, 335, 339
acutatum Schott 330
acutifolium K. Krause 334
adhatodifolium Schott 334
adrena Schott 317, 318, 319, 320, 332, 333, 334, 339, 344, 349, 353, 357, 358, 359, 363, 366, 368, 369, 370, 371, 376, 379, 390, 391–393, 505, 517, 529, 570, 573, 577, 589, 598, 697
affine Hemsl. 397, 543
albisuccus Croat 311, 331, 339, 353, 355, 357, 376, 386, 393–394, 570, 573, 577, 590
alticola Croat & Grayum .. 311, 322, 331, 339, 355, 356, 358, 360, 370, 386, 394–395, 425, 524, 534, 570, 573, 577, 591
amplectans A. C. Sm. 413
andreanum Devansaye 331, 336, 447
angustialatum Engl. 334
angustilobum Croat & Grayum .. 311, 322, 336, 338, 345, 350, 354, 355, 357, 358, 359, 362, 379, 396–397, 490, 570, 573, 577, 592, 598
angustinum K. Koch 318, 507
angustisectum Engl. 337
anisotomum Schott ... 316, 317, 318, 319, 320, 336, 338, 345, 351, 352, 353, 355, 357, 358, 361, 369, 370, 379, 383, 397–400, 544, 565, 570, 573, 577, 587, 590, 593, 598
annulatum Croat & Grayum 311, 322, 333, 339, 348, 349, 350, 351, 353, 355, 357, 370, 383, 384, 386, 387, 388, 400–402, 517, 559, 570, 573, 577, 594
antonioanum Croat ... 311, 331, 339, 347, 348, 351,

353, 356, 357, 358, 359, 360, 365, 376, 402–403, 550, 570, 573, 577, 595
apocarpum Matuda 318, 320, 469
arcuatum K. Krause 331, 412
armigerum Standl. & L. O. Williams 319, 565
aromaticum Croat & Grayum 311, 322, 333, 339, 353, 355, 357, 358, 359, 377, 390, 402–404, 453, 565, 570, 573, 579, 596
asperatum K. Koch 329
augustinum K. Koch 317
aurantiifolium Schott 315, 316
auriculatum Standl. & L. O. Williams 318, 319, 334, 339, 346, 348, 350, 351, 352, 355, 358, 359, 362, 369, 377, 385, 404–406, 434, 500, 559, 570, 573, 577, 582, 584, 585, 596, 597
auritum Lindl. 565
bahiense Engl. 327
bakeri Croat & Grayum 311, 321, 322, 334, 339, 349, 350, 351, 355, 356, 357, 366, 369, 376, 383, 406–407, 452, 518, 570, 575, 577, 599
barrosoanum G. S. Bunting 335, 336, 337, 490
basii Matuda 318, 319, 320, 333, 339, 342, 352, 353, 355, 356, 357, 376, 377, 387, 407–408, 570, 573, 577, 600
bertae K. Krause 329
billietiae Croat 330
bipinnatifidum Schott ex Endl. 361, 371, 372, 373
blanchetianum Schott 328
brandtianum K. Krause 329
breedlovei Croat 311, 312, 331, 339, 357, 358, 360, 376, 377, 388, 389, 390, 409, 437, 529, 570, 573, 577, 599, 601
brenesii Standl. 318, 319, 320, 321, 333, 339, 351, 355, 358, 361, 365, 369, 370, 390, 409–412, 426, 444, 570, 573, 577, 588, 601, 602
brevilaminatum Schott 329, 444
brevinodum Standl. & L. O. Williams 319, 565
brevispathum Schott 316, 317, 319, 330, 331, 337, 338, 343, 345, 357, 361, 369, 378, 379, 388, 412–413, 470, 570, 573, 577, 602
subsp. *holmquistii* (G. S. Bunting) G. S. Bunting 412, 413
brewsterense Croat 311, 312, 334, 339, 349, 352, 354, 355, 357, 359, 376, 383, 413–414, 570, 573, 577, 413–414, 602
brunneicaule Croat & Grayum 311, 322, 329, 338, 345, 350, 351, 352, 353, 354, 355, 357, 358, 378, 388, 389, 414–416, 421, 570, 573, 577, 603, 604
bulaoanum Engl. 335, 337, 339
buntingianum Croat 334
burle-marxii G. Barroso 368
callosum K. Krause 327, 328, 361
subsp. *ptarianum* (Steyerm.) G. S. Bunting 327
canaimae G. S. Bunting 327
cataniapoense G. S. Bunting 335, 336
chimantae G. S. Bunting 445
chimboanum Engl. 327
chiriquense Croat 311, 327, 331, 339, 344, 345, 347, 349, 353, 356, 357, 376, 386, 416–417, 421, 570, 573, 577, 604, 606
chirripoense Croat & Grayum 311, 312, 321, 329, 331, 344, 349, 352, 354, 355, 357, 359, 365, 376, 377, 383, 417–418, 491, 570, 573, 577, 605
clematis Wright in Griseb. 329, 444
clewellii Croat 311, 335, 339, 351, 355, 357, 359, 389, 390, 418–419, 570, 573, 577, 605
coerulescens Engl. 318, 328
colombianum R. E. Schult. 455
coloradense Croat 311, 333, 339, 353, 376, 388, 390, 419–420, 570, 572, 577, 605, 606
conforme G. S. Bunting 581
consanguineum Schott 329, 332
copense Croat 311, 329, 338, 344, 349, 350, 353, 354, 355, 356, 357, 358, 359, 365, 385, 386, 415, 417, 420–421, 496, 570, 573, 577, 607, 608
corcovadense Kunth 344
cordatum hort. non Vell. 459
correae Croat 311, 334, 339, 350, 351, 354, 355, 357, 361, 364, 367, 376, 383, 401, 421–422, 443, 480, 570, 573, 577, 608, 609
cotobrusense Croat & Grayum 311, 312, 322, 336, 338, 352, 353, 355, 357, 376, 377, 382, 422–423, 487, 514, 544, 545, 570, 573, 577, 609
cotonense Croat & Grayum 311, 335, 339, 345, 350, 356, 357, 367, 369, 388, 390, 423–425, 561, 570, 573, 577, 606, 610
craspedodromum R. E. Schult. 327
crassinervium Lindl. 326, 327
crassispathum Croat & Grayum 311, 319, 321, 322, 333, 339, 350, 353, 355, 357, 358, 359, 363, 369, 370, 387, 410, 414, 425–427, 570, 573, 577, 607, 610, 611, 617
cretosum Croat & Grayum 311, 322, 328, 331, 339, 349, 353, 355, 360, 365, 384, 394, 427–428, 570, 573, 577, 611, 615
cuneatum Engl. 328, 512
cuspidatum K. Koch & Bouché 459, 460
cyrtocoleum F. Diels 334
daemonum Liebm. 316, 317, 320, 516
dagilla Schott 316, 397, 399
daguense Linden & André 553
davidsonii Croat 318, 319, 320, 333, 339, 345, 349, 350, 351, 353, 357, 358, 359, 360, 362, 363, 366, 384, 385, 428–429, 582
subsp. *davidsonii* Croat 348, 355, 429–430, 570, 573, 577, 612, 613
subsp. *bocatoranum* Croat 311, 351, 357, 365, 385, 429, 430, 570, 573, 577, 584, 612, 613
deltoideum Poepp. & Endl. 327
demerarae Gleason 444
devansayeanum L. Linden 432
deviatum Schott 332, 335, 469
discolor K. Krause 553
distantilobum K. Krause 337
dodsonii Croat & Grayum 311, 322, 331, 335, 339, 345, 347, 352, 355, 357, 359, 360, 376, 378, 379, 386, 387, 430–432, 435, 453, 524, 570, 573, 577, 614, 615, 617
dolichophyllum Croat 311, 322, 334, 339, 351, 353, 355, 357, 360, 370, 384, 432–434, 570, 573, 577, 616, 617
dolosum Schott 329
dominicalense Croat & Grayum 311, 335, 339, 355, 376, 377, 387, 570, 573, 577, 431, 434–435, 618
donnell-smithii Engl. 527
dressleri G. S. Bunting 318, 319, 320, 321, 338, 344, 347, 351, 353, 354, 355, 357, 365, 376, 377, 382, 435–436, 507, 510, 557, 570, 573, 577, 617, 619
dunstervilleorum G. S. Bunting 327
dwyeri Croat 311, 312, 322, 333, 339, 352, 353, 357, 359, 364, 376, 377, 390, 436–437, 570, 573, 577, 618
dyscarpium R. E. Schult. var. *dyscarpium* 327

ecuadorense Engl. 539
edenudatum Croat 311, 333, 339, 345, 350, 354, 357, 360, 376, 388, 437–438, 453, 454, 570, 573, 577, 618, 620
effusilobum Croat 335, 336
eichleri Engl. 372
elaphoglossoides Schott 334
elegans K. Krause 337
ellipticum Engl. 327
englerianum Steyerm. 328
erlansonii I. M. Johnst. 318, 320, 469
ernestii Engl. 329, 415
erubescens Linden 332
fenderli K. Krause 328, 337
fenzlii Engl. 317, 318, 543, 545
ferrugineum Croat 311, 333, 339, 344, 350, 351, 353, 355, 359, 360, 364, 369, 370, 376, 378, 390, 438–440, 453, 486, 570, 573, 577, 621, 623, 626, 697
fibrillosum Poepp. 328, 334, 345
findens Croat & Grayum 311, 319, 322, 329, 338, 345, 349, 351, 352, 354, 355, 356, 357, 358, 359, 360, 369, 370, 382, 385, 440–442, 502, 524, 570, 573, 577, 581, 588, 622, 623, 624
folsomii Croat 311, 312, 334, 339, 353, 355, 357, 376, 384, 442–443, 551, 570, 573, 577, 620, 623
fortunense Croat 311, 329, 338, 345, 349, 350, 352, 353, 357, 389, 443–444, 571, 573, 577, 624, 625
fragrantissimum (Hook.) G. Don 320, 328, 329, 338, 341, 344, 349, 357, 359, 360, 363, 365, 369, 376, 378, 379, 385, 444–446, 571, 573, 577, 587, 626, 627
fragrantissimum (Hook.) Kunth 316, 317, 318
fraternum Schott 330
fuertesii K. Krause 329
giganteum Schott 330, 339, 585
gigas Croat 311, 330, 331, 336, 339, 344, 346, 348, 349, 351, 352, 353, 355, 356, 357, 359, 360, 376, 386, 446–447, 571, 573, 577, 627, 628, 631
glanduliferum Matuda 317, 318, 319, 320, 321, 338, 342, 347, 348, 350, 351, 352, 355, 357, 371, 379, 447–449, 488, 573, 624
subsp. *glanduliferum* 331, 379, 387, 448, 571, 577, 629, 630
subsp. *camiloanum* Croat 448, 629
gloriosum André 336, 444
goeldii G. M. Barroso 342, 351
gracile Schott 315, 316, 317, 318, 320, 539
grandifolium (Jacq.) Schott 315, 330, 380
grandipes K. Krause 317, 318, 319, 329, 331, 338, 339, 342, 345, 347, 348, 349, 350, 353, 354, 357, 359, 360, 361, 363, 369, 374, 376, 378, 379, 380, 387, 449–451, 473, 571, 574, 577, 630, 631, 633
granulare Croat 311, 334, 339, 353, 355, 357, 364, 368, 369, 370, 384, 451–452, 571, 574, 577, 631, 697
graveolens Engl. 327
grayumii Croat 311, 322, 333, 339, 345, 351, 353, 354, 355, 356, 357, 360, 361, 370, 388, 419, 420, 431, 438, 440, 452–454, 571, 574, 577, 632, 633
gualeanum Engl. 331
guatemalense Engl. 317
guttiferum Kunth 317, 319
hammelii Croat 311, 312, 331, 338, 342, 345, 350, 357, 376, 387, 454–455, 488, 532, 555, 571, 574, 577, 634
harlowii I. M. Johnst. 318, 320, 460
hastiferum Standl. & L. O. Williams 319, 565
hebetatum Croat 311, 330, 339, 347, 351, 352, 353, 355, 357, 359, 360, 362, 368, 378, 379, 455, 536, 542, 571, 574, 577, 588, 634, 636
hederaceum (Jacq.) Schott 314, 315, 316, 317, 318, 319, 320, 329, 330, 332, 335, 338, 341, 343, 345, 353, 357, 358, 360, 363, 364, 365, 369, 370, 376, 377, 378, 379, 385, 388, 389, 458–460, 470, 504, 635
var. *hederaceum* 317, 343, 344, 378, 460, 460–463, 464, 571, 574, 577, 635
var. *hederaceum* f. *micans* 317, 318
var. *kirkbridei* Croat 311, 321, 348, 378, 388, 460, 463–464, 571, 574, 577, 635
var. *oxycardium* (Schott) Croat 311, 316, 317, 318, 377, 460, 464–465, 571, 574, 578
hederaceum sensu Kunth 340
heleniae Croat 311, 335, 339, 345, 349, 350, 353, 355, 356, 357, 359, 360, 362, 370, 377, 378, 380, 384, 465–467, 478, 570, 574, 578, 636, 637
heterophyllum Poepp. 334
hoffmannii Schott 316, 317, 319, 320, 332, 337
hoffmannii Schott sensu Engl. 318, 459, 469
holtonianum Schott 335, 336, 546
holmquistii G. S. Bunting 412
houlettiana Engl. 337
hylaeae G. S. Bunting 335, 336
imbe Schott 331
immixtum Croat 311, 334, 339, 343, 345, 349, 350, 351, 352, 353, 355, 357,360, 362, 364, 365, 378, 379, 383, 384, 407, 467–469, 481, 551, 570, 574, 578, 638
impolitum Schott 316, 507
inaequilaterum Liebm. 315, 317, 328, 369
inconcinnum Schott 364, 468
jacquinii Schott 316, 317, 318, 319, 320, 332, 335, 337, 338, 341, 343, 345, 349, 357, 363, 364, 365, 369, 370, 376, 378, 379, 388, 389, 413, 459, 460, 469–471, 571, 574, 578, 637, 639, 640
jamapanum G. S. Bunting 318, 320, 391
jefense Croat 311, 312, 333, 339, 353, 357, 366, 370, 376, 387, 471–472, 477, 571, 574, 578, 639
jenmanii K. Krause 330, 335
jodavisianum G. S. Bunting 318, 319, 320, 321, 331, 339, 340, 347, 349, 350, 353, 357, 359, 360, 361, 362, 363, 378, 379, 386, 450, 472–475, 495, 542, 571, 574, 578, 640, 641, 643
juninense Engl. 328
karstedianum Schott 319
knappiae Croat 311, 333, 339, 342, 349, 355, 357, 359, 365, 376, 390, 411, 475, 571, 574, 578, 639, 640, 642, 643
krebsii Schott 329
lacerum (Jacq.) Schott 315, 337
laciniosum Schott 315
lancigerum Standl. & L. O. Williams 319, 516, 518
latilobum Schott 336
latipes K. Koch & Augustin 444
latisagittium Matuda 319, 320, 489
lazorii Croat 311, 322, 331, 339, 347, 352, 353, 360, 387, 472, 476–477, 495, 571, 574, 578, 583, 642, 643, 644
leal-costae Mayo & G. M. Barroso 344
lechlerianum Schott 329, 498, 504
lehmannii Engl. 327
lentii Croat & Grayum 311, 321, 333, 339, 342,

349, 352, 354, 355, 457, 369, 383, 384, 466, 477–479, 484, 493, 571, 574, 578, 645, 646
levelii G. S. Bunting 336, 337
liesneri G. S. Bunting 334
ligulatum Schott 316, 317, 318, 320, 334, 339, 345, 349, 350, 351, 355, 357, 359, 360, 362, 397, 401, 422, 468, 479–481, 500, 559
var. *ligulatum* 354, 357, 378, 379, 380, 384, 480, 481, 481–482, 484, 500, 571, 574, 578, 646, 647
var. *heraclioanum* Croat 311, 334, 349, 353, 357, 364, 367, 384, 480, 481, 482, 482–483, 500, 559, 571, 574, 578, 648
var. *ovatum* Croat 311, 334, 349, 357, 360, 383, 480, 481, 482, 483–484, 571, 574, 578, 647, 648
limnestis Dilcher & Daghlian 322
lindenii Schott 332, 334, 336
lingulatum (L.) K. Koch 315, 481
linnaei Kunth 327, 344
llanense Croat ... 311, 322, 331, 339, 349, 350, 356, 360, 362, 370, 386, 387, 439, 484–486, 524, 571, 574, 578, 646, 649
longilaminatum Schott 327
longipes Engl. 327
longipetiolatum Engl. 334
longistilum K. Krause 338
lundellii Bartlett ex Lundell 319, 470
madronense Croat 311, 312, 336, 338, 351, 352, 354, 357, 376, 382, 423, 486–487, 545, 571, 574, 578, 649
maguirei G. S. Bunting 540
malesevichiae Croat .. 311, 331, 338, 342, 345, 350, 351, 357, 360, 378, 380, 385, 487–489, 555, 571, 574, 578, 580, 585, 586, 650
mamei André 336, 447
marginatum Urb. 329
maximum K. Krause 329
megalophyllum Schott 330, 342, 351, 369, 370, 582, 584, 585, 586
melanochrysum Linden & André 329
melinonii Brongn. ex Regel 328, 337
mexicanum Engl. 317, 318, 319, 320, 333, 339, 342, 345, 352, 354, 357, 358, 359, 360, 362, 363, 370, 378, 379, 383, 388, 389, 397, 489–490, 571, 574, 578, 651
micans K. Koch 315, 316, 317, 318, 329, 459, 460
micranthum Poepp. ex Schott 327
microphyllum K. Koch 461
microstictum Standl. & L. O. Williams 319, 335, 339, 349, 351, 352, 353, 354, 355, 357, 358, 369, 377, 383, 418, 490, 538, 571, 574, 578, 652
miduhoi Matuda 319, 320, 459, 460
mirificum Standl. & L. O. Williams 319, 501
monticola Matuda 319, 320, 391, 392
morii Croat 311, 334, 339, 352, 353, 365, 370, 377, 384, 492–493, 571, 574, 578, 652
multispadiceum Engl. 335
muricatum Willd. ex Schott 330, 335, 413
muschlerianum K. Krause 329
myrmecophyllum Engl. & Schenck 334
nanegalense Engl. 331
niqueanum Croat 311, 333, 339, 348, 353, 355, 365, 367, 376, 377, 385, 493, 571, 574, 578, 653
obtusilobum Miq. 336
ornatum Schott 329, 330, 338, 350, 448
oxycardium Schott 315, 316, 317, 318, 329, 459, 460, 464
oxyprorum Schott 461
pachycaule K. Krause 327
pachyphyllum K. Krause 334
panamense K. Krause 317, 318, 319, 320, 330, 331, 339, 348, 351, 352, 353, 355, 357, 358, 360, 362, 365, 376, 386, 387, 473, 477, 493–495, 526, 571, 574, 578, 654
panduriforme (Kunth) Kunth 327, 336
pastazanum K. Krause 336
paxianum K. Krause 327
pedatum (Hook.) Kunth 337
peraiense G. S. Bunting 327
phlebodes G. S. Bunting 327
pilatonense Engl. 331, 553
pimichinense G. S. Bunting 327
pinnatifidum (Jacq.) Schott 315, 328, 337
pirrense Croat 311, 331, 339, 347, 348, 350, 353, 354, 357, 376, 387, 495–496, 571, 574, 578, 655, 656
pittieri Engl. 317, 318, 320, 335, 377, 461
platypetiolatum Madison ... 319, 320, 333, 339, 350, 352, 353, 355, 357, 378, 379, 388, 496, 498, 571, 574, 578, 656
pleistoneurum Standl. & L. O. Williams 319, 449
polytomum Schott 316, 318, 507
poeppigii Schott 444
populneum K. Koch 332
prieurianum Schott 329, 459
pseudauriculatum Croat 311, 322, 334, 339, 348, 351, 352, 355, 358, 359, 369, 378, 380, 384, 405, 433, 434, 483, 498–501, 552, 571, 574, 578, 588, 654, 657, 658
pseudoradiatum Matuda 319, 320, 510
ptarianum Steyerm. 327, 328, 361
pterotum K. Koch & Augustin .. 316, 317, 318, 319, 320, 329, 331, 338, 345, 349, 352, 357, 359, 360, 361, 363, 376, 379, 385, 441, 501–503, 571, 574, 578, 657, 658
pulchrum G. M. Barroso 327
purpureoviride Engl. 317, 318, 330, 338, 345, 347, 353, 357, 369, 370, 376, 378, 389, 459, 503–504, 538, 571, 574, 578, 659
purpureoviridis 317, 329
purulhense Croat 311, 319, 320, 331, 339, 350, 352, 353, 355, 357, 358, 359, 370, 376, 379, 387, 392, 504–506, 517, 572, 574, 578, 660, 661
quitense Engl. 330
radiatum Schott 316, 317, 318, 319, 320, 321, 337, 338, 342, 349, 352, 354, 355, 357, 360, 361, 363, 364, 367, 370, 374, 376, 377, 379, 436, 506, 507, 537, 557, 580, 660
var. *radiatum* 349, 378, 382, 507, 507–510, 572, 574, 578, 662, 663
var. *pseudoradiatum* (Matuda) Croat 311, 319, 320, 337, 357, 377, 382, 436, 507, 510, 537, 572, 574, 578, 581, 661, 662
reichenbachianum Schott 327
remifolium R. E. Schult. 327
robustum Schott 328
robustum Sodiro ined. 432
roraimae K. Krause 328
roseospathum Croat ... 311, 328, 331, 341, 347, 349, 350, 353, 355, 360, 366, 370, 384, 511–512, 666
var. *rosespathum* ... 342, 512, 513, 572, 574, 578, 665

var. *angustilaminatum* Croat 311, 312, 359, 512, 513, 572, 574, 578, 667
rothschuhianum (Engl. & K. Krause) Croat & Grayum ... 336, 338,345, 348, 351, 352, 357, 358, 359, 360, 361, 370, 379, 382, 513–516, 572, 574, 578, 580, 582, 663, 664, 666
rubens Schott ... 329, 330, 336
ruizii Schott ... 334
sabulosum G. S. Bunting ... 327
sagittifolium Liebm. 316, 317, 318, 319, 320, 332, 333, 342, 349, 350, 353, 353, 354, 360, 361, 362, 364, 365, 369, 370, 376, 378, 379, 390, 392, 404, 407, 516–521, 537, 545, 550, 552, 553, 565, 572, 574, 578, 666, 667, 668
sagittifolium Schott ... 316, 339, 401
cf. *sagittifolium* ... 518
sanguineum Regel ... 317, 318, 320, 516, 518
scabrum K. Krause ... 330, 335
scalarinerve Croat & Grayum ... 311, 322, 331, 339, 347, 349, 350, 353, 355, 356, 358, 360, 378, 380, 384, 521–523, 572, 574, 578, 669, 670
scandens K. Koch & Sello ... 315, 316, 317, 318, 329, 377, 459, 460, 491
f. *micans* (Schott) G. S. Bunting ... 460
subsp. *oxycardium* (Schott) G. S. Bunting ... 464
var. *cuspidatum* (K. Koch & Bouché) Engl. ... 460
schottianum H. Wendl. ex Schott ... 317, 318, 320, 330, 331, 339, 345, 347, 348, 350, 351, 352, 353, 356, 357, 358, 359, 360, 361, 385, 386, 387, 396, 435, 485, 486, 523–525, 524, 542, 572, 574, 578, 580, 584, 671, 672
seguine Schott ... 315, 317
selloum K. Koch ... 372, 373
serpens Hook. f. ... 331, 530
simsii (Hook.) Don ... 328
smithii Engl. ... 317, 318, 320, 334, 335, 339, 345, 350, 351, 353, 359, 360, 361, 364, 368, 369, 370, 379, 389, 390, 525–528, 561, 572, 575, 578, 670, 672, 673, 674
sodiroanum Engl. ... 539
sodiroi hort. ... 336
solimoesense A. C. Sm. ... 342, 346
sonderianum Schott ... 361
sousae Croat ... 311, 312, 333, 339, 352, 357, 359, 364, 366, 376, 377, 389, 409, 528–529, 572, 575, 578, 674
speciosum Schott ... 372
sphalerum Schott ... 442, 468, 492
splitgerberi Schott ... 329
squamicaule Croat & Grayum ... 311, 331, 338, 342, 345, 347, 350, 352, 353, 354, 355, 357, 358, 365, 366, 378, 380, 385, 529–531, 555, 572, 575, 578, 673, 675
squamipetiolatum Croat ... 311, 331, 338, 345, 350, 352, 354, 357, 365, 378, 380, 383, 389, 447, 455, 488, 531–532, 555, 572, 575, 578, 673, 676
standleyi Grayum ... 370
steyermarkii G. S. Bunting ... 327
straminicaule Croat ... 311, 322, 335, 339, 344, 345, 351, 353, 355, 358, 359, 364, 386, 390, 394, 395, 410, 526, 532–534, 561, 572, 575, 578, 581, 673, 677
strictum G. S. Bunting ... 319, 321, 330, 339, 347, 353, 355, 359, 360, 370, 378, 379, 385, 456, 457, 534–536, 542, 572, 575, 578, 678, 679
subhastatum Engl. & K. Krause ... 334
subincisum Schott ... 316, 333, 339, 345, 350, 352, 353, 360, 365, 377, 388, 536–537, 572, 575, 578, 678, 680
subovatum Schott ... 317, 318, 332, 334, 391
sulcicaule Croat & Grayum ... 311, 321, 335, 339, 343, 345, 352, 353, 354, 355, 357, 362, 388, 389, 537–539, 572, 575, 578, 679, 680
surinamense (Miq. ex Schott) Engl. ... 368
talamancae Engl. ... 317
tanyphyllum Schott ... 316, 516
tatei K. Krause ... 327
tenue K. Koch & Augustin ... 315, 316, 317, 318, 320, 330, 331, 339, 348, 349, 350, 351, 352, 357, 360, 378, 379, 388, 539–541, 572, 575, 578, 680, 681, 683
tenuipes Engl. ... 334, 428
thalassicum Croat & Grayum ... 311, 321, 322, 330, 339, 349, 350, 351, 354, 355, 385, 386, 456, 524, 536, 540, 541–543, 572, 575, 578, 681, 682, 683
thaliifolium Schott ... 329
tobagoense Engl. ... 329
trauni Engl. ... 329
tripartitum (Jacq.) Schott ... 315, 316, 317, 318, 319, 320, 326, 336, 338, 345, 350, 352, 355, 359, 361, 362, 364, 367, 368, 378, 379, 382, 398, 399, 423, 487, 514, 543–549, 572, 575, 578, 683, 684, 685
var. *tricuspidatum* Engl. ... 543
trisectum Standl. ... 319, 320, 397
tuxtlanum G. S. Bunting ... 320, 516
tysonii Croat ... 311, 322, 333, 339, 348, 352, 353, 356, 357, 359, 361, 370, 387, 388, 402, 403, 419, 549–551, 572, 575, 578, 587, 686, 687
ubigantupense Croat 311, 312, 334, 339, 349, 355, 359, 376, 377, 383, 551, 572, 575, 578, 688
uleanum Engl. ... 334
urbanianum K. Krause ... 329
utleyanum Croat ... 311, 312, 334, 339, 355, 357, 367, 384, 551–552, 572, 575, 579, 687
validinervium Engl. ... 410
verapazense Croat ... 311, 312, 319, 320, 333, 339, 345, 352, 355, 357, 379, 389, 552–553, 572, 575, 579, 688
verrucosum L. Mathieu ex Schott ... 316, 317, 318, 320, 331, 338, 345, 350, 353, 357, 358, 365, 377, 378, 379, 385, 387, 447, 488, 530, 531, 553–556, 572, 575, 579, 689, 691
victoriae G. S. Bunting ... 336, 337
viride Engl. ... 334
wallisii Regel ex Engl. ... 336
warszewiczii K. Koch & Bouché ... 316, 317, 320, 321, 325, 337, 338, 342, 345, 347, 348, 349, 350, 351, 352, 353, 357, 359, 364, 365, 366, 367, 369, 370, 379, 382, 408, 436, 507, 556–558, 572, 575, 579, 583, 690, 691, 692, 697
weberbaueri Engl. ... 334
wendlandii Schott ... 315, 317, 318, 319, 320, 327, 334, 338, 339, 345, 351, 355, 358, 360, 363, 369, 377, 379, 385, 481, 500, 558–559, 572, 575, 579, 583, 692, 693
wilburii Croat & Grayum ... 311, 321, 322, 335, 339, 345, 348, 362, 369, 370, 389, 377, 388, 475, 492, 504, 526, 559–561, 562
var. *wilburii* ... 319, 321, 357, 377, 561–563, 572, 575, 579, 692, 693, 694
var. *longipedunculatum* Croat & Grayum ... 311, 321, 352, 353, 358, 366, 389, 525, 534, 561, 562, 563–564, 572, 575, 579, 694, 695
williamsii Hook. f. ... 372

wittianum Engl. 334
wurdackii G. S. Bunting 334
zhuanum Croat 311, 333, 339, 350, 353, 356, 357, 360, 364, 388, 390, 564–565, 572, 575, 579, 696
Philodendrum Schott 315, 380, 576
Piptospatha N. E. Br. 322
Pistia L. 314
Pothos L. 314
Rhodospatha Poepp. 326, 353
Sauromatum venosum Kunth 373
Schismatoglottis Zoll. & Moritzi 324
Spathantheum Schott 323
Spathicarpa Hook. 323
Spathiphyllum Schott 315, 324, 353
Sphincterostigma [unranked] 324
Stenospermation Schott 353
Synandrospadix Engl. 323
Syngonium (Engl.) Croat 314, 315, 343, 370, 565
armigerum (Standl. & L. O. Williams) Croat 319, 565
hastiferum (Standl. & L. O. Williams) Croat 319, 565
rothschuhianum Engl. 513
Taccarum Brongn. ex Schott 323
Telipodus Raf. 380
grandifolius (Jacq.) Raf. 380
Thaumatophyllum Schott 380
spruceanum Schott 380
Typhonodorum Schott 322, 360
Xanthosoma Schott 370
undipes (K. Koch & Bouché) K. Koch 374
Zantedeschia Spreng. 314, 360

Volume 84, Number 3, pp. 311–704 of the Annals of the Missouri Botanical Garden
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Petioles ... 349
Blades ... 351
Blade Shape ... 351
Posterior Lobes ... 352
Sinus Shape ... 352
Blade Size ... 352
Venation ... 353
Midribs ... 353
Primary Lateral Veins ... 354
Basal Veins ... 354
Posterior Ribs ... 354
Lesser Order Veins ... 355
Morphology of Reproductive Structures ... 356
Inflorescences ... 356
Peduncles ... 357
Spathes ... 358
Spathe Color ... 359
Spadix ... 362
Male Flowers ... 363
Pollen ... 363
Female Flowers ... 363
Placentation ... 364
Ovary Locule Number ... 365
Ovules per Locule ... 365
Style and Stigma Morphology ... 366
Style Types ... 367
Fruits and Seeds ... 368
Pollination Biology ... 370
Breeding Behavior ... 374
Phenology ... 375
A. Flowering in Dry Season and Wet Season ... 376
B. Flowering only in Wet Season ... 376
C. Flowering only in Dry Season ... 376
D. Flowering All Year ... 376
E. Flowering Bimodally ... 377
Cytology ... 377
Geographical Distribution and Endemism ... 377
Taxonomic Treatment ... 380
Generic Description ... 380
Key to Subgenera of *Philodendron* ... 380
Subgeneric Description ... 380
Keys to Species of *Philodendron* Subg. *Philodendron* ... 382
Species Descriptions ... 391
Excluded Names ... 565
Literature Cited ... 566
Appendix 1: Geographic Distribution of Central American *Philodendron* Subg. *Philodendron* ... 570
Appendix 2: Technical Data on Pistils ... 573
Appendix 3: Composition of *Philodendron* Subg. *Philodendron* in Central America 576
Appendix 4: Phenological Patterns of Central American *Philodendron* ... 577
Figures ... 580
Index ... 698

CONTENTS

A Revision of *Philodendron* Subgenus *Philodendron* (Araceae) for Mexico and Central America *Thomas B. Croat* 311
Abstract 311
Introduction 312
Materials and Methods 312
Acknowledgments 313
History of the Genus *Philodendron* 314
Heinrich Wilhelm Schott 314
Adolf Engler 316
Kurt Krause 317
Modern Work 318
Collecting History 321
Fossil History 322
Intrageneric Relationships 322
Infrageneric Relationships 324
Key to Subgenera of *Philodendron* 325
Relationships Within *P.* Subg. *Philodendron* 326
Discussion of Subgeneric Classification 326
1. *P.* Sect. *Baursia* 326
2. *P.* Sect. *Philopsammos* 327
3. *P.* Sect. *Philodendron* 328
1. *P.* Subsect. *Macrolonchium* (328); 2. *P.* Subsect. *Canniphyllum* (328); 3. *P.* Subsect. *Platypodium* (329); 4. *P.* Subsect. *Psoropodium* (329); 5. *P.* Subsect. *Solenosterigma* (329); 6. *P.* Subsect. *Philodendron* (330); 7. *P.* Subsect. *Achyropodium* (331) 328
4. *P.* Sect. *Calostigma* 331
1. *P.* Subsect. *Macrobelium* (332); 2. *P.* Subsect. *Glossophyllum* (334); 3. *P.* Subsect. *Oligocarpidium* (335); 4. *P.* Subsect. *Bulaoana* (335); 5. *P.* Subsect. *Eucardium* (336) 332
5. *P.* Sect. *Tritomophyllum* 336
6. *P.* Sect. *Schizophyllum* 337
7. *P.* Sect. *Polytomium* 337
8. *P.* Sect. *Macrogynium* 337
9. *P.* Sect. *Camptogynium* 338
Key to Sections and Subsections of *P.* Subg. *Philodendron* 338
Morphology of Vegetative Structures 340
Anatomy 340
Vegetative Anatomy (by R. C. Keating) 340
Vascular Anatomy 341
Habit and Growth Patterns 342
Stems 344
Petiolar Scars 345
Roots 346
Cataphylls 347
Leaves 348

Contents continued on inside back cover

Cover illustration. *Eccremocarpus viridis* Ruiz & Pavón, by Phyllis Bick.

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A REVISION OF *STYRAX* (STYRACACEAE) FOR WESTERN TEXAS, MEXICO, AND MESOAMERICA[1]

Peter W. Fritsch[2]

ABSTRACT

Despite a recent taxonomic treatment of *Styrax* from North America and the Caribbean, the taxonomy of this genus has remained poorly understood. In an effort to clarify the taxonomy of *Styrax* from western Texas through Mesoamerica, morphological characteristics of over 2500 specimens from 29 herbaria were examined. The previous treatment emphasized vegetative characters for circumscription, whereas the present revision includes heretofore poorly characterized features of the androecium. This revision comprises 19 species and 24 taxa in the area considered, nearly three times as many species as recognized previously. It includes six new species (*S. gentryi, S. incarnatus, S. nicaraguensis, S. radians, S. steyermarkii, S. tuxtlensis*), two new subspecies (*S. platanifolius* subsp. *mollis, S. nicaraguensis* subsp. *ellipsoidalis*), three new combinations (*S. platanifolius* subsp. *stellatus, S. platanifolius* subsp. *texanus, S. platanifolius* subsp. *youngiae*), and two new species names (*S. austromexicanus, S. lanceolatus*). Two names (*S. glabrescens* var. *pilosus* and *S. jaliscanus*) are lectotypified. Nearly 70% of the species recognized in the revision are narrow endemics. This work has provided the basis for a taxonomic revision of all neotropical *Styrax* that is currently under way.

The genus *Styrax* comprises about 120 species of trees and shrubs distributed in eastern and southeastern Asia, the New World, and the Mediterranean region. It is a member of the family Styracaceae (12 genera, about 150 species), which, along with the Ebenaceae, Lissocarpaceae, Sapotaceae, and, according to some authors, the Symplocaceae, comprise the order Ebenales (Cronquist, 1981; Dahlgren, 1980; Takhtajan, 1980, 1987; Thorne, 1992). A phylogenetic analysis of the Ebenales based on chloroplast DNA *rbc*L sequences (Morton et al., 1997) tentatively indicates that Styracaceae are diphyletic, with *Styrax* sister to *Clethra* (of the monotypic Clethraceae). *Styrax* has essentially a Laurasian Tertiary relict distribution (as defined in Tiffney, 1985) except for a large neotropical component and a single species that extends east of Wallace's Line to New Guinea and

[1] I thank the curators of the following herbaria, who kindly made specimens available: A, AAU, B, BH, BR, CAS, CHAPA (one specimen), CR, DS, DUKE, F, GH, HCIB, IBUG, INB, K, LL, MEXU, MICH, MO, MSC, NY, POM, RSA, TEX, U, US, W, and WIS. I am indebted to Lisa K. Fritsch for help with the collection database, Porter P. Lowry II, Paul S. Manos, Stephen A. Spongberg, and Robert L. Wilbur for helpful comments on the manuscript, and Lisa Bush for illustrations. This work was supported by a grant from the A. W. Mellon Foundation and Duke University.

[2] Department of Botany, Duke University, Durham, North Carolina 27708-0339, U.S.A. Current address: Department of Botany, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118-4599, U.S.A.

several islands of the South Pacific (Perkins, 1907; van Steenis, 1932; Fritsch, 1995). The genus is characterized by a campanulate, white or pink, usually 5-parted corolla with petals connate at the base, usually twice the number of stamens as petals, a 3-locular, superior ovary, a linear style, and a 1–3-seeded drupe, nut, or 3-valved capsule with a persistent calyx. Leaf arrangement is alternate, and the vesture consists of scales or stellate hairs.

Infrageneric Classification

Styrax is currently divided into section *Foveolaria* (Ruiz & Pav.) Perkins, comprising taxa with 3- to 5-ovulate gynoecia (two species, Cuba and Peru), and section *Styrax*, with 16- to 24-ovulate gynoecia (all the remaining species; Perkins, 1907). Perkins (1907) maintained two series within section *Styrax*: series *Imbricatae* Gürke (about 30 species) and series *Valvatae* Gürke (about 90 species). As the names suggest, the species of series *Imbricatae* possess imbricate corolla aestivation, and those of series *Valvatae* possess valvate corolla aestivation. However, some species of section *Valvatae* are variable for aestivation type—sometimes even within the same individual (Perkins, 1907). For this reason van Steenis (1932) suggested that the two series are not "natural" (i.e., monophyletic) but offered no alternative classification. A recent study of the internal transcribed spacer regions of nuclear ribosomal DNA (Fritsch, 1995, 1996a) has supported the non-monophyly of the two series, but because of limited sampling in this study, the development of a revised classification at this time is premature.

Ongoing morphological studies of *Styrax* (Fritsch, unpublished data) suggest that characters in addition to corolla aestivation are important in the delimitation of infrageneric categories. The 60 or so neotropical evergreen *Styrax* species possess a drupe, although the fruit is nearly always mistakenly described in the literature as dry, hard-walled, and rugose because of the appearance of immature fruits on herbarium specimens (the mature fruit is rarely collected). The rest of the genus has dry fruits: in the paleotropical evergreen taxa they are thick-walled and either indehiscent or dehiscent via three valves; in the deciduous taxa of the northern subtropical and north-temperate zones they are thin-walled and usually dehiscent via three valves (rarely they are indehiscent). Corolla aestivation is valvate in all neotropical and paleotropical evergreen species, but valvate and/or imbricate in the deciduous species (Fritsch, 1995). On the basis of these characters, the delimitation of neotropical evergreen, paleotropical evergreen, and deciduous groups within *Styrax* appears to be justified. Additional phylogenetic work in the genus using both morphological and molecular characters is needed to lay the groundwork for a revised infrageneric classification.

Prior Work on Mesoamerican *Styrax* and Present Objectives

The present taxonomic revision was undertaken in conjunction with a treatment of Styracaceae in the ongoing series *Flora Mesoamericana*. There are two modern (20th century) treatments of *Styrax* in Mesoamerica (the region east of the Isthmus of Tehuantepec south through Panama) for use as reference works for the *Flora Mesoamericana* treatment. The first (Perkins, 1907) provided a treatment of the species of the region as part of a worldwide monograph of the Styracaceae and is the most recent worldwide treatment of *Styrax* to date. Perkins (1907) recognized six species from the region: *S. argenteus, S. conterminus, S. glabrescens, S. polyanthus, S. polyneurus,* and *S. warscewiczii.* The second (Gonsoulin, 1974) comprised part of a revision of North American, Central American, and Caribbean *Styrax*. In this treatment, the number of species in this region was reduced to three: *S. argenteus, S. conterminus,* and *S. glabrescens.* As a basis for this reduction, Gonsoulin (1974) argued (with some justification) that Perkins was a notorious splitter who disregarded continuous character variation. Gonsoulin (1974) also placed several new species that had been described subsequent to Perkins's (1907) monograph in synonymy under *S. argenteus.* Gonsoulin's revision, having been based on much more data than Perkins's, initially appeared to provide an adequate context for undertaking the *Flora Mesoamericana* treatment.

However, it became clear during early examination of Mesoamerican material that Gonsoulin (1974) had made a number of problematic taxonomic decisions, particularly concerning the circumscription of *S. argenteus.* This species was divided into three loosely defined varieties that encompassed all evergreen *Styrax* in Mexico and Mesoamerica except *S. conterminus,* which possesses an unusual trichome type easily delimiting it from the rest of the material examined by Gonsoulin. He justified this circumscription by comparing it with the variable nature of the characters used in Perkins's (1907) key to differentiate additional species, specifically pubescence on the lower laminar surface, flower length, and calyx length. I agree with Gonsoulin (1974) that these characters by themselves provide poor support for species cir-

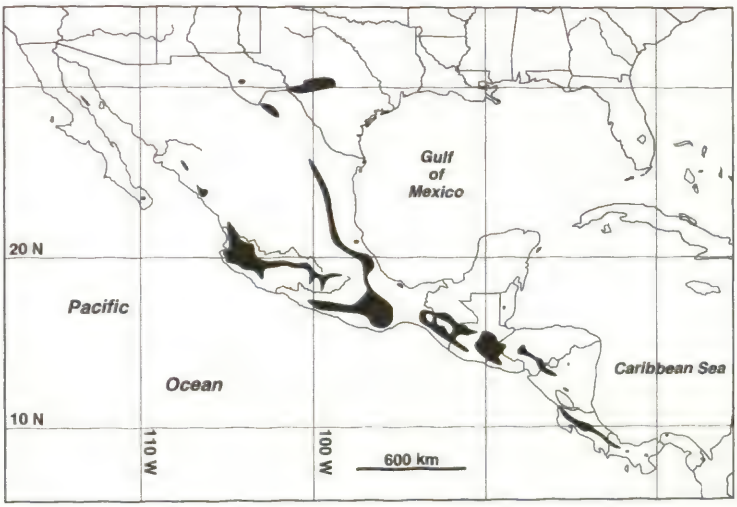


Figure 1. General distribution of *Styrax* in western Texas, Mexico, and Mesoamerica.

cumscription in *Styrax*, and it is unfortunate that Perkins provided only these characters in her key, because she included a number of critical androecial characters in her descriptions that at once distinguish *S. argenteus* from many of those taxa placed in synonymy by Gonsoulin. Apparently Gonsoulin surmised that, because she rarely included them in her key, Perkins considered androecial characters inconsequential. On this basis, he apparently decided not to pursue the potential utility of androecial characters for circumscription, for he did not employ them in the key to species or describe them to any significant degree.

The questionable concepts of circumscription in Gonsoulin (1974) were compounded by various nomenclatural and bibliographic errors in the same work, making the application of names to taxa I had recognized in the Mesoamerican region uncertain. Although Perkins's (1907) treatment was careful, I considered this work outdated and the species concepts within it too narrow for reliable use. Therefore, I decided to examine not only material from Mesoamerica, but also all *Styrax* material from western Texas and Mexico, as well as a limited amount of South American material, to provide the general context for a clear and unambiguous treatment for *Flora Mesoamericana*.

Geographic Distribution, Endemism, and Ecology

Styrax exhibits a somewhat discontinuous distribution in western Texas, Mexico, and Mesoamerica (Fig. 1). The northern half of the range can be divided into two parts. In the northeastern part of the region members of the genus occur from the Edwards Plateau and the Davis Mountains of Texas south along the Sierra Madre Oriental to Oaxaca; in the northwestern part they extend from the Cape Region of Baja California Sur and southern Sinaloa to Oaxaca along the western slope of the Sierra Madre Occidental, the southern slope of the trans-Mexican volcanic belt, and the Sierra Madre del Sur, bypassing the low elevations of the Río Balsas basin. Collections are also known from the Tuxtlas Range in Veracruz. The southern half of the range extends from the Sierra Madre and Central Plateau of Chiapas through the mountainous regions of Guatemala, northwestern El Salvador, and Honduras to a small portion of northern Nicaragua, and then along the Pacific slope of the cordillera from extreme southern Nicaragua to western Panama. Isolated localities have been recorded in Belize, central Nicaragua, and central and eastern Panama.

The 19 species of *Styrax* recognized in this treatment are all endemic to the region of interest except *S. glabratus* and *S. peruvianus*, both of which also occur in South America. Only six species are relatively widespread and fairly common: *S. argenteus, S. glabratus, S. glabrescens, S. radians, S. ramirezii,* and *S. warscewiczii.* Nearly all the rest are narrow endemics and are likely to be rare, vulnerable, endangered, or extinct (terms sensu Lucas & Synge, 1978). Two species are known with certainty only from single collections (i.e., *S. tuxtlensis, S. panamensis*). *Styrax platanifolius* has a relatively large range but is uncommon; it comprises five subspecies, all of which are rare. In contrast, *S. magnus* occurs only from central Chiapas to southwest-

ern Guatemala yet has been collected many times; thus it is probably common within its narrow range, although it is unclear to what extent sampling artifact has affected the perceived abundance of this and other species. Locating additional populations of all narrow endemics, especially *S. gentryi, S. incarnatus, S. panamensis, S. steyermarkii,* and *S. tuxtlensis,* will be invaluable for comprehensive documentation of morphological features, biogeographic studies, and conservation.

Species of *Styrax* are found most often from 500 to 2500 m elevation. Several species (*S. argenteus, S. glabratus, S. panamensis, S. radians*) occur additionally or exclusively at elevations < 500 m; others (*S. austromexicanus, S. glabratus, S. ramirezii, S. warscewiczii*) extend to 3000 m elevation or more. According to herbarium specimen information, the genus is most often associated with *Quercus* and *Pinus* but can occur in a wide variety of forested situations, such as tropical humid forests, subtropical deciduous forests, seasonal evergreen forests, temperate deciduous forests, coffee plantations, and open savannas. *Styrax platanifolius* subsp. *youngiae* grows in woodlands composed of *Acer, Arbutus, Cercis, Juniperus,* and *Quercus* (*Wendt 582*), and also those composed of *Pinus* (piñon) and *Juniperus* (*Johnston et al. 11888*). Many species show a distinct preference for mesic microhabitats, such as canyons, draws, and other riparian situations. However, individuals of various *Styrax* species are also found in less protected situations, such as pastures and wind-swept ledges. Within primary forests, the tree species (i.e., all except *S. jaliscanus* and *S. platanifolius*) are usually understory or mid-canopy trees, seldom attaining a height of > 20 m. They also occur in secondary forests and other disturbed situations such as roadsides, burned-over areas, plantations, and open fields.

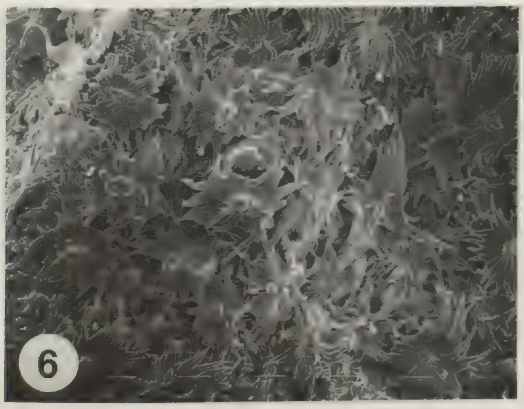
Locating populations of *Styrax* species in the field using herbarium label information can be difficult, primarily because they generally are local, sporadic, and normally small (< 30 individuals). Furthermore, members of the genus lack easily observable diagnostic features that would otherwise facilitate identification at a distance. The smooth or cracked gray bark and alternate, simple leaves with entire margins typical of the evergreen members of the genus are similar to many associates, e.g., *Ocotea* of the Lauraceae.

The deciduous species of *Styrax* generally flower in April and May and produce mature fruit by September; however, at low latitude they appear to possess a broader range of flowering and fruiting times. In contrast, the evergreen species flower and fruit at variable times throughout the year. The factors controlling flowering times are unknown. The fruits in the deciduous group (and likely in the evergreen group) take several months to mature; in the evergreen group, maturation from the green, relatively hard phase of fruit development to the purplish black, fleshy mature phase is not synchronous within an infructescence, and change of single fruits to the fleshy phase likely occurs quickly (within days).

Some neotropical species (*S. argenteus, S. glabratus, S. nicaraguensis, S. panamensis,* and *S. steyermarkii* in the present treatment) bear relatively long and stiff, stellate hairs that form a dense mass on the ventral side of the distinct portion of each stamen filament (Figs. 11, 12). The arms of the hairs are predominantly oriented along the longitudinal axis of the flower. A high proportion of the arms belonging to hairs nearest the distal end of the filament point upward; these are usually the longest in the hair mass (0.8–2 mm long). In the same location on each filament, two longitudinally oriented auricles can occur (*S. argenteus, S. nicaraguensis, S. peruvianus,* and *S. steyermarkii* in the present treatment; Figs. 12, 13). They are usually obscured by the dense hair mass that surrounds them; in *S. peruvianus* the trichome arms (in this case, scales) are relatively short and the auricles are larger and more prominent than those of the other species in the treatment (Fig. 13). The dense hairs and auricles occupy much of the space within the stamen tube and partially cover the ovary. The auriculate and densely pubescent conditions are both probably derived within *Styrax*: the genus *Pamphilia* Mart., likely the sister group to *Styrax,* lacks auricles and pubescence. In the floral bud stage, the auricles and/or pubescence occupy the cavity between the basal end of the anther and the apex of the ovary, and therefore may help to protect the bud from small herbivores.

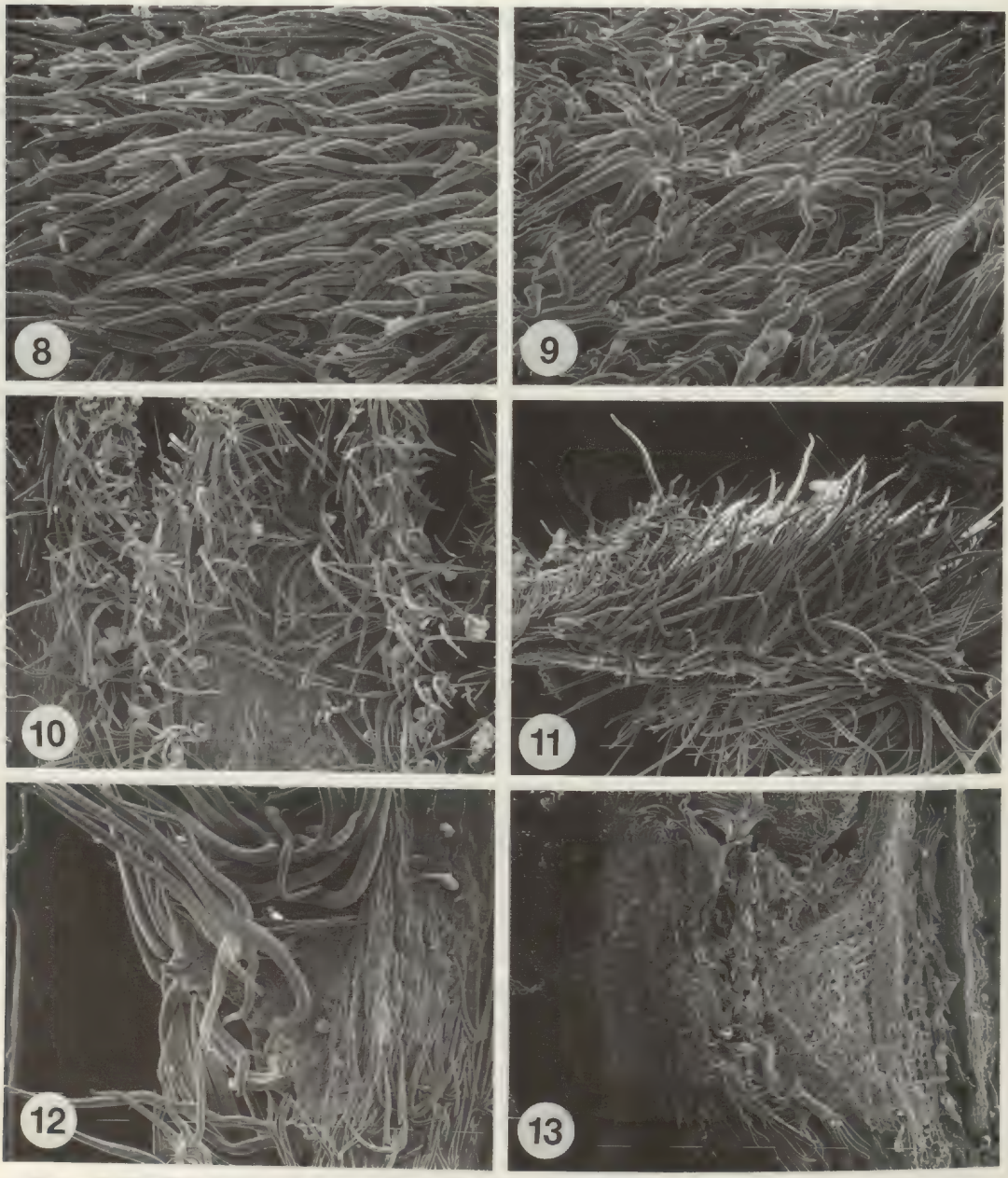
In all other species of *Styrax* treated here, the ventral side of the distinct portion of the stamen filament lacks both auricles and a mass of stiff-armed stellate hairs, and the hairs nearest the distal end of the filaments are not noticeably longer nor do they have predominantly upward-pointing arms. The pubescence that is present is instead short-armed (to ± 0.7 mm long) and situated mainly along the filament margins (Fig. 10). The face of the filament proper (as opposed to the margin) is often glabrous proximally, becoming sparsely to densely pubescent distally.

Little comparative work has been done on the reproductive biology of *Styrax* species, especially those within the region of study. The most detailed analysis of breeding systems and pollination biology in the genus has been conducted by Sugden



Figures 2–7. SEM micrographs of the calyx vesture in various *Styrax* taxa from Mexico and Mesoamerica. —2. *Styrax argenteus, Breedlove 28487* (DS). —3. Stellate form of *Styrax ramirezii, McVaugh 11766* (MICH). —4. Small-scaled form of *Styrax ramirezii, Koch & Sánchez 7929* (MO). —5. *Styrax warscewiczii, Breedlove & Thorne 30989* (DS). —6. *Styrax steyermarkii, Steyermark 48666* (F). —7. *Styrax conterminus, Matuda 5507* (NY). Small divisions of scale bar = 90 μm in 2, 4–6, and 83 μm in 3, 7.

(1986) on *S. redivivus* (Torr.) L. C. Wheeler [referred to by Sugden (1986) as *S. officinale* subsp. *redivivum* (Torr.) Thorne], endemic to California. Bagging experiments showed the study population to be xenogamous. Plants were determined to be almost exclusively entomophilous, despite sucrose-dominant nectar; rarely, the flowers were visited by hummingbirds. The most common visitor was the non-native honeybee *Apis mellifera*, individuals of which were observed to forage for pollen and nectar (as did most of the bee genera that were seen to visit the species). The most efficacious pollinators



Figures 8–13. SEM micrographs of corolla vesture (8, 9) and the distinct portion of the stamen filament (10–13) in various *Styrax* taxa from Mexico and Mesoamerica. —8. Large-scaled form of *Styrax ramirezii, Conzatti 2450* (F). —9. *Styrax warscewiczii, Breedlove & Thorne 30989* (DS). —10. *Styrax warscewiczii, Breedlove & Thorne 30989* (DS). —11. *Styrax panamensis, Pittier 4242* (NY). —12. *Styrax argenteus, Breedlove 28487* (DS). —13. *Styrax peruvianus, Croat 37190* (NY). Small divisions of scale bar = 9.1 μm in 8, 8.3 μm in 9, and 90 μm in 10–13.

were butterflies of the genus *Battus*. Other common visitors were the bumble bees *Bombus edwardsii* and *B. vosnesenskii*, and the carpenter bee *Xylocopa tabaniformis*. Stellate hairs on the outer surface of the petals and on the androecium appeared to aid insect pollinators, which grasped them for support in the process of foraging. Nectar-foraging honeybees were often observed to wedge their way down against the base of the style to reach the nectaries. During this process the stigma was pushed away from the bee and did not contact it. This was considered by Sugden (1986) to be a form of nectar

"thieving," because the flower was not pollinated by the insect during this process even though it relinquished its reward.

It is not known whether the pollination syndrome documented in *S. redivivus* is typical of other *Styrax* species. Because evolution of floral morphology in *Styrax* has been conservative, the general syndrome of bee and butterfly pollination combined with xenogamy might be expected to apply across much of the genus. The flower-visiting fauna of *S. redivivus* resembles that of *S. americanus* Lam. and *S. grandifolius* Aiton, both from the southeastern United States, and sucrose-dominant nectar is also produced by *S. argenteus* (Sugden, 1986). Morphological gynodioecy has been documented for the genus *Pamphilia* (Miers, 1859) and has recently been observed (pers. obs.) in the two species of *Styrax* comprising section *Foveolaria* (*S. foveolaria* Perkins and *S. obtusifolius* Griseb.). These two *Styrax* species might be expected to exhibit a pollination syndrome divergent from that of most or all other species in the genus. Additional study of the pollination and breeding systems of a wide variety of *Styrax* species (including those of sect. *Foveolaria*) and *Pamphilia* would provide further insight into the evolution of reproductive systems in the genus.

Materials and Methods

Over 2500 herbarium specimens from 29 herbaria were examined for this study. South American material from BR, BM, CAS, F, GH, MICH, MO, NY, P, US, and W, and Asian material from GH were also examined to aid in understanding the taxonomic significance of character variation in the Mesoamerican members of the genus and to determine whether the taxa recognized here occur also in other regions. One week of fieldwork in Texas (*S. platanifolius* subspp. *stellatus* and *texanus*) and two weeks in southwestern Mexico (*S. jaliscanus* and *S. radians*) supplemented observations on the herbarium specimens.

All descriptions were derived from examination of herbarium specimens except where noted. Flowering and fruiting times, elevation ranges, habitats, distributions, common names, and uses were derived from label information of herbarium specimens. Descriptions of leaves refer to those of the fertile branches; leaves of sterile branches are consistently larger and often possess more variation in hair quantity and quality than those of fertile branches. Leaf and petiole measurements were taken from the larger examples on each herbarium sheet. All floral descriptions refer to the anthesis stage only, except where noted. Calyx dimensions are presented in terms of height (from the end of the pedicel to the apical margin) × width at the apex, and thus include the short hypanthium. Measurements of corolla length do not include the hypanthium. In the descriptions, the phrase "free portion of the stamen tube" refers to the section of the androecium from where it becomes free from the corolla to where the filaments become distinct (i.e., free from each other). Fruit length was measured from the base of the fruiting calyx to the tip of the fruit (the calyx is persistent). Fruit measurements of the drupe-bearing species were taken from the larger examples on each fruiting branch of fully expanded but unripe fruits (fully mature drupes are rarely present on herbarium specimens); those of the dry-fruited species were taken from the larger examples of mature fruits. Most observations were made by eye or with the aid of a dissecting microscope (maximum magnification = 60×). Examination of trichome morphology was supplemented with SEM.

Seven infraspecific taxa are recognized in the present treatment. The category "subspecies" has been used in all cases in accordance with the concepts of Hultén (1967) and Thorne (1978). These authors use the subspecies category for infraspecific taxa that are geographically as well as morphologically distinct.

Taxonomic Treatment

The following taxonomic treatment of *Styrax* from southern North America differs substantially from that of Gonsoulin (1974). A comparison using only Gonsoulin's annotated material shows that nearly three times as many species are recognized in the present revision as the last (Appendix 1). The number of deciduous species is lower (three vs. five) and the number of evergreen species is much higher (ten vs. two). Specimens representing six additional species were collected or accessioned subsequent to publication of the last revision (Appendix 1). The total number of species and taxa circumscribed in the present revision is 19 and 24, respectively, versus 7 and 11 in the last revision (Appendix 1). Therefore, the genus is much more diverse in Mexico and Mesoamerica than previously thought. Six new species and two new subspecies are described. In addition, three new combinations and two new species names result from this study.

Styrax L., Sp. pl. 444. 1753. TYPE: *Styrax officinalis* L. ["*officinale*"].

Strigilia Cav., Diss. 7: 358, t. 201. 1789. *Tremanthus* Pers., Syn. pl. 1: 467. 1805. TYPE: *Strigilia racemosa* Cav.

Cyrta Lour., Fl. cochinch. Ed. 1: 278. 1790. TYPE: *Cyrta agrestis* Lour.

Foveolaria Ruiz & Pav., Fl. peruv. prodr. 57, t. 9. 1794. TYPE: [not designated].

Adnaria Raf., Fl. ludov. 56. 1817. TYPE: *Adnaria odorata* Raf.

Epigenia Vell., Fl. flumin. 183. 1829. TYPE: [not designated].

Benzoin Hayne, Getreue Darstell. Gew. 11, t. 24. 1830, non Boerh. ex Schaeff., 1760. TYPE: *Benzoin officinalis* Hayne [= *Styrax benzoin* Dryand.].

Darlingtonia Torr., Proc. Amer. Assoc. Advancem. Sci. 4: 191. 1851, nom. rej. TYPE: *Darlingtonia rediviva* Torr.

Evergreen or deciduous trees or shrubs; bark smooth or cracked, gray; outer layer of older twigs fibrous, dull brown or more often gray, inner layer dull maroon; buds superposed, lepidote or stellate-pubescent, naked. Vesture consisting of scales, stalked or unstalked stellate hairs, and often sessile or stalked glandular hairs; evergreen species usually with inconspicuous scattered stalked glandular hairs on at least some of the vegetative parts: often adaxially on petiole and base of laminar midrib, abaxially on laminar surface, and on inflorescence bracteoles. Leaves alternate, simple, pinnately nerved, estipulate. Inflorescences bracteolate, axillary or false-terminal racemes or panicles, sometimes corymbose in appearance, sometimes two or more arising from the same node (or a single inflorescence branched at the base), sometimes 1–2-flowered, then usually axillary. Flowers actinomorphic, bisexual or rarely gynodioecious, fragrant, with a short hypanthium adnate to the basal third or less of the ovary wall; calyx gamosepalous beyond the hypanthium, campanulate or cupuliform, teeth (2–)4–6 or absent; corolla gamopetalous beyond the hypanthium proximally, the petals distinct distally, campanulate, the lobes 5(–10) and almost always longer than the tube, valvate or imbricate in bud, white, pink, or rarely yellow; stamens adnate to the corolla tube beyond the hypanthium proximally, free distally, 10 when the number of corolla lobes = 5, up to twice the number of the corolla lobes when the number of lobes > 5, uniseriate but appearing biseriate in bud (with five stamens in each series), the inner series often exceeding the outer at the distal end of the androecium, free portion of the filaments often connate proximally and distinct distally, sometimes completely distinct, the ventral side of the distinct portion glabrous to stellate-pubescent or lepidote and sometimes with two juxtaposed and longitudinally oriented auricles, these often obscured by a dense mass of hairs, many of which have arms predominantly oriented along the longitudinal axis of the flower, the hairs nearest the distal end of the filaments with arms predominantly pointing upward; anthers introrse, 2-locular, basifixed, longitudinally dehiscent, the anther sacs glabrous to moderately stellate-pubescent; pollen light or golden yellow; ovary superior, 3-locular at base, 1-locular toward apex; style filiform, slightly exceeding the stamens; stigma terminal, obscure, capitate or ± 3-lobed; ovules (3–5)16–24, axile or basal, anatropous. Fruit a drupe, a capsule dehiscent via 3 valves, or nut-like (dry and indehiscent), globose or ellipsoid, 1(–3)-seeded, with calyx persistent. Seed globose or ellipsoid, brown, completely filling the fruit cavity, usually smooth except for 3(–6) longitudinal grooves, with a broad hilum; endosperm copious; embryo straight; cotyledons flattened. About 120 species. U.S.A. to Argentina, E Mediterranean, E and SE Asia.

Note. The generic name *Styrax* has been treated by various authors as masculine, feminine, or neuter. Nicolson and Steyskal (1976), after conducting a thorough evaluation of the issue, advocated the use of masculine as the gender that best fits the wording of the botanical rules of nomenclature. Thus, *Styrax* is treated as masculine here.

Key to Species of *Styrax* in Texas, Mexico, and Mesoamerica

1a. Corolla lobes imbricate in bud, partly overlapping at anthesis; fruit dry, indehiscent or dehiscent via three valves; plants deciduous (*Styrax* sect. *Styrax* ser. *Imbricatae*).
- 2a. Trees to 30 m tall, small individuals not multi-stemmed from the base; lamina membranous; fruit nearly always indehiscent, rarely dehiscent via three valves, the larger fruits 10–17 mm long ..... 6. *S. glabrescens*
- 2b. Shrubs to 3 m tall, multi-stemmed from the base; lamina chartaceous; fruit dehiscent by three valves, the larger fruits 7–11 mm long.
  - 3a. Longer petioles 4–5 mm long; leaf bases subcuneate or rounded, rarely subcordate but then not attenuate; secondary and tertiary laminar veins prominent abaxially; undehisced fruit wall coarsely and weakly longitudinally striate, not transversely wrinkled post-dehiscence ..... 8. *S. jaliscanus*
  - 3b. Longer petioles 6–20 mm long; some leaf bases on each plant cordate or truncate and slightly attenuate; secondary and tertiary laminar veins evident but not prominent abaxially; undehisced fruit wall smooth, usually transversely wrinkled post-dehiscence ..... 14. *S. platanifolius*

1b. Corolla lobes valvate in bud, non-overlapping at anthesis; fruit a drupe; plants evergreen (*Styrax* sect. *Styrax* ser. *Valvatae*).
- 4a. Abaxial laminar surface (and calyx) with vesture of peltate or lacerate-margined scales; scales at mid-calyx 0.27–0.44 mm diam.
  - 5a. Ventral side of the distinct portion of the stamen filaments not auriculate; leaves 2.8–3.9 times

as long as wide; connectives not or only slightly prolonged beyond the non-tapered anther sacs ..... 3. *S. conterminus*

5b. Ventral side of the distinct portion of the stamen filaments strongly auriculate; leaves 2.0–3.1 times as long as wide; connectives distinctly prolonged beyond the tapered anther sacs ..... 13. *S. peruvianus*

4b. Abaxial laminar surface with vesture of stellate hairs, or rarely radiate scales or nearly glabrous; scales at mid-calyx 0.05–0.33 mm diam., or else lacking.

6a. Leaf bases distinctly oblique ..... 18. *S. tuxtlensis*

6b. Leaf bases symmetric or only slightly oblique.

7a. Arms of the hairs nearest the distal end of the ventral side of the distinct portion of the stamen filaments predominantly pointing upward, some of these up to (0.8–)1–2 mm long; connectives distinctly prolonged beyond the tapered anther sacs.

8a. Calyx vesture uniformly golden brown; lamina 1.5 times as long as wide ..... 12. *S. panamensis*

8b. Calyx vesture predominantly or completely grayish green, occasionally with additional scattered yellow or orange-brown trichomes; lamina 2.1–3.8(–5.2) times as long as wide.

9a. Calyx vesture of stellate hairs.

10a. Larger upward-pointing hairs on the ventral side of the distinct portion of the stamen filaments with at least some arms 1–2 mm long; abaxial laminar surface and outer calyx grayish green-stellate-pubescent, without scattered orange-brown stellate hairs; larger drupes 13–18 mm long (excluding beak, if present), ellipsoid or ovoid-ellipsoid; corolla lobes 1.7–2.3 mm wide, widely spreading or recurved ..... 1. *S. argenteus*

10b. Larger upward-pointing hairs on the ventral side of the distinct portion of the stamen filaments with arms to 1 mm long; abaxial laminar surface and outer calyx with scattered, orange-brown, stellate hairs in addition to grayish green pubescence; larger drupes (15–)17–28 mm long, ovoid or obovoid; corolla lobes 2.5–4 mm wide, recurved or reflexed ..... 11. *S. nicaraguensis*

9b. Calyx vesture of radiate scales.

11a. Abaxial laminar surface glabrous or nearly so; calyx 4–7 mm long, in fruit funnelform, 4–8 mm long; anthers 5–8 mm long; corolla lobes linear-deltoid ..... 5. *S. glabratus*

11b. Abaxial laminar surface densely pubescent; calyx 2.5–3 mm long, in fruit shallowly cupuliform, to 1.5 mm long; anthers 4.5 mm long; corolla lobes linear ..... 17. *S. steyermarkii*

7b. Arms of the hairs nearest the distal end of the ventral side of the distinct portion of the stamen filaments not predominantly pointing upward, typically not exceeding 0.5(–0.7) mm long; connectives not or only slightly prolonged beyond the non-tapered anther sacs.

12a. Calyx teeth 1–2 mm long, contiguous ..... 4. *S. gentryi*

12b. Calyx teeth 0–0.6 mm long, not contiguous.

13a. Vesture just below mid-calyx of radiate scales.

14a. Vesture on the outer distal third of the corolla lobes of stellate hairs; anthers 3.0–4.8 mm long, 1.9–5.3 times as long as the distinct portion of the filaments ..... 16. *S. ramirezii*

14b. Vesture on the outer distal third of the corolla lobes of radiate scales; anthers 1.7–3.6 mm long, 1.1–2.2 times as long as the distinct portion of the filaments ..... 19. *S. warscewiczii*

13b. Vesture just below mid-calyx predominantly of stellate hairs, sometimes also with a few scale-like hairs scattered among the stellate ones.

15a. Abaxial surface of the secondary and tertiary veins obscured by the tomentum; ± evenly scattered, orange-brown hairs (in addition to whitish pubescence) present on the abaxial surface of most or all fully expanded leaves.

16a. Laminae chartaceous, lanceolate, the larger 7.7–9.7 cm long; fruit 9–11 mm long; corolla 11–15(–17) mm long, white ..... 9. *S. lanceolatus*

16b. Laminae thick-chartaceous, elliptic, slightly oblanceolate, or ovate, the larger 11–18 cm long; fruit 17–19 mm long (unknown in *S. incarnatus*); corolla (10–)14–24 mm long, usually pink, sometimes white.

17a. Larger laminae 3.5–5 cm wide, usually narrowly elliptic, sometimes slightly oblanceolate, slightly ovate, or elliptic; lower pedicels 11–15 mm long; calyx 4–5 × 5–6 mm ..... 2. *S. austromexicanus*

17b. Larger laminae 5.5–9.5 cm wide, ovate or broadly elliptic; lower pedicels 3–9 mm long; calyx 3–3.5 × 2.5–4.5 mm ..... 7. *S. incarnatus*

15b. Abaxial surface of the secondary and tertiary veins evident; orange-brown hairs on the abaxial surface of fully expanded leaves at most sporadically present on some of the veins, otherwise nearly always absent.
18a. Larger fruits 15–20 × 9–12 mm; lamina usually obovate, sometimes broadly elliptic ..... 10. *S. magnus*
18b. Larger fruits 7–15 × 5–9 mm; lamina ovate-oblong or elliptic, sometimes lanceolate, suborbicular, or ovate.
19a. Distinct portion of stamen filaments 2.5–3.5 mm long; abaxial laminar surface usually soft to the touch; calyx not stellate-villous; corolla white, thin, the petals connate up to the calyx margin, the lobes moderately or widely spreading; stigma 0.6–0.8 mm wide ..... 15. *S. radians*
19b. Distinct portion of stamen filaments 0.6–2.0(–2.6) mm long; abaxial laminar surface slightly or moderately rough or rarely soft to the touch, if soft then at least the lower third of the calyx villous; corolla white or pink, thickened, the petals connate 1–3 mm beyond the calyx margin distally, the lobes slightly spreading; stigma 0.3–0.5 mm wide ..... 16. *S. ramirezii*

1. Styrax argenteus C. Presl, Reliq. haenk. 2: 60. 1831–1835. *Strigilia argentea* (C. Presl) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 282. 1859. TYPE: Mexico. Guerrero: "Ad portum et urbem Acapulco" (protologue), *T. Haenke s.n.* (or *148*; Perkins, 1907) (holotype, PR not seen; isotypes, F, MO, W, photo of W in A, F, MICH). Figures 2, 12, 14–16.

Styrax myristicifolius Perkins, Bot. Jahrb. Syst. 31: 481. 1902. TYPE: Guatemala. Santa Rosa: Las Viñas, Sep. 1894, *Heyde & Lux 6182* (lectotype, designated by Standley & Williams (1967), F; isolectotypes, GH, MO, NY, US).

Styrax polyanthus Perkins, Bot. Jahrb. Syst. 31: 479. 1902. TYPE: Guatemala. Guatemala: prope Guatemala, February 1890, *J. Donnell Smith 2266* (lectotype, designated by D'Arcy (1979), US; isolectotypes, F, GH).

Evergreen tree to 20(–30) m. Young twigs grayish yellow-, yellowish brown-, light brown-, or orange-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 10–25 mm long. Lamina chartaceous, 6.5–18 × 2.4–7.5 cm, 2.1–3.7 times as long as wide, ovate, lanceolate, narrowly or broadly elliptic, or rarely slightly oblanceolate, secondary veins 9–11; apex acute to acuminate; base cuneate to rounded, often slightly attenuate, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute grayish green stellate hairs and often also larger, soft, grayish green or yellowish brown stellate hairs, the minute hairs usually absent from the primary through tertiary veins, thus the vein surface easily visible; margin entire. Inflorescences axillary or false-terminal, racemose or rarely paniculate, the racemes or panicle branches 3–14 cm long, 3–22-flowered. Lower pedicels 2–11(–15) mm long. Calyx 2.5–5.0 × (3.5–)4–6(–7) mm, cupuliform or broadly cupuliform, grayish green-stellate-pubescent; calyx teeth 5, to 0.5 mm long, deltoid, calyx margin truncate or rarely slightly concave between the teeth, inner margin often glandular. Corolla white, 10–16 mm long, petals usually connate up to the calyx margin, rarely to 2 mm distally beyond; corolla lobes 5, valvate in bud, 8–14 × 1.7–2.3 mm, non-overlapping, widely spreading or recurved, thin, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0.7–1 mm long; distinct portion of filament 2–2.5 mm long, of equal width throughout, ventrally with small auricles bearing a dense mass of white stellate, stiff hairs with at least some arms 1–2 mm long, the hairs nearest the distal end of the filament with arms predominantly pointing upward, also pubescent below the auricles and at the sinus between adjacent filaments; anthers (5–)6–8 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely stellate-hirsute; style glabrous, or pubescent at base only; stigma 0.3–0.5 mm wide. Drupe 13–18 × 8–14 mm (wider when 2-seeded; does not include occasional beak), ellipsoid or ovoid-ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Near Acapulco, Guerrero, Mexico, to central Panama; most common on the Pacific slope of the cordillera of Central America; one collection from Cayo District, Belize; 100–1700 m; tropical humid forests, seasonal evergreen forests with *Pinus* and *Quercus*, tropical deciduous forests, pastures, open scrub, coffee plantations; found often along waterways with other riparian vegetation, and in moist ravines, but also on dry limestone ridges, at forest edges, disturbed slopes, and with various types of

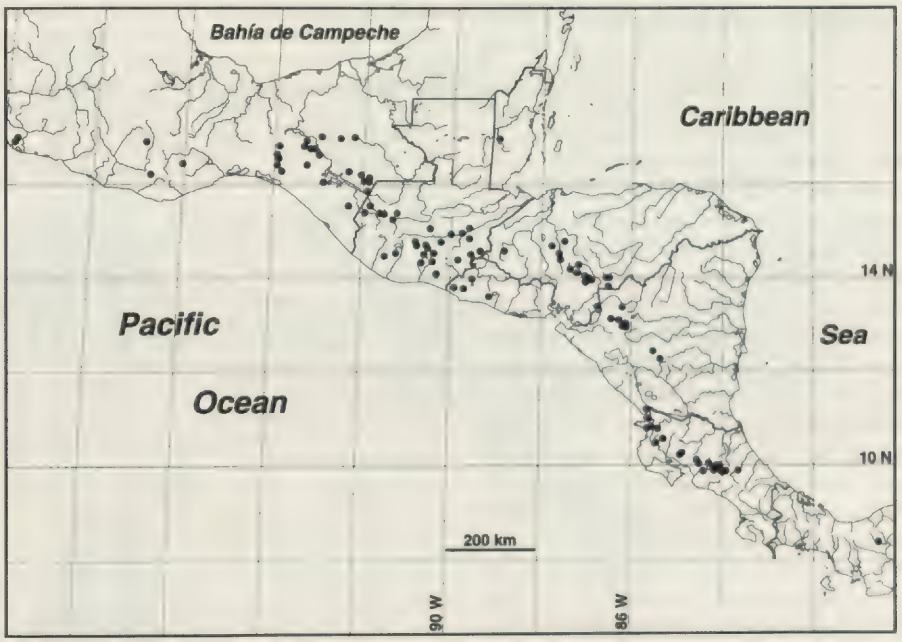


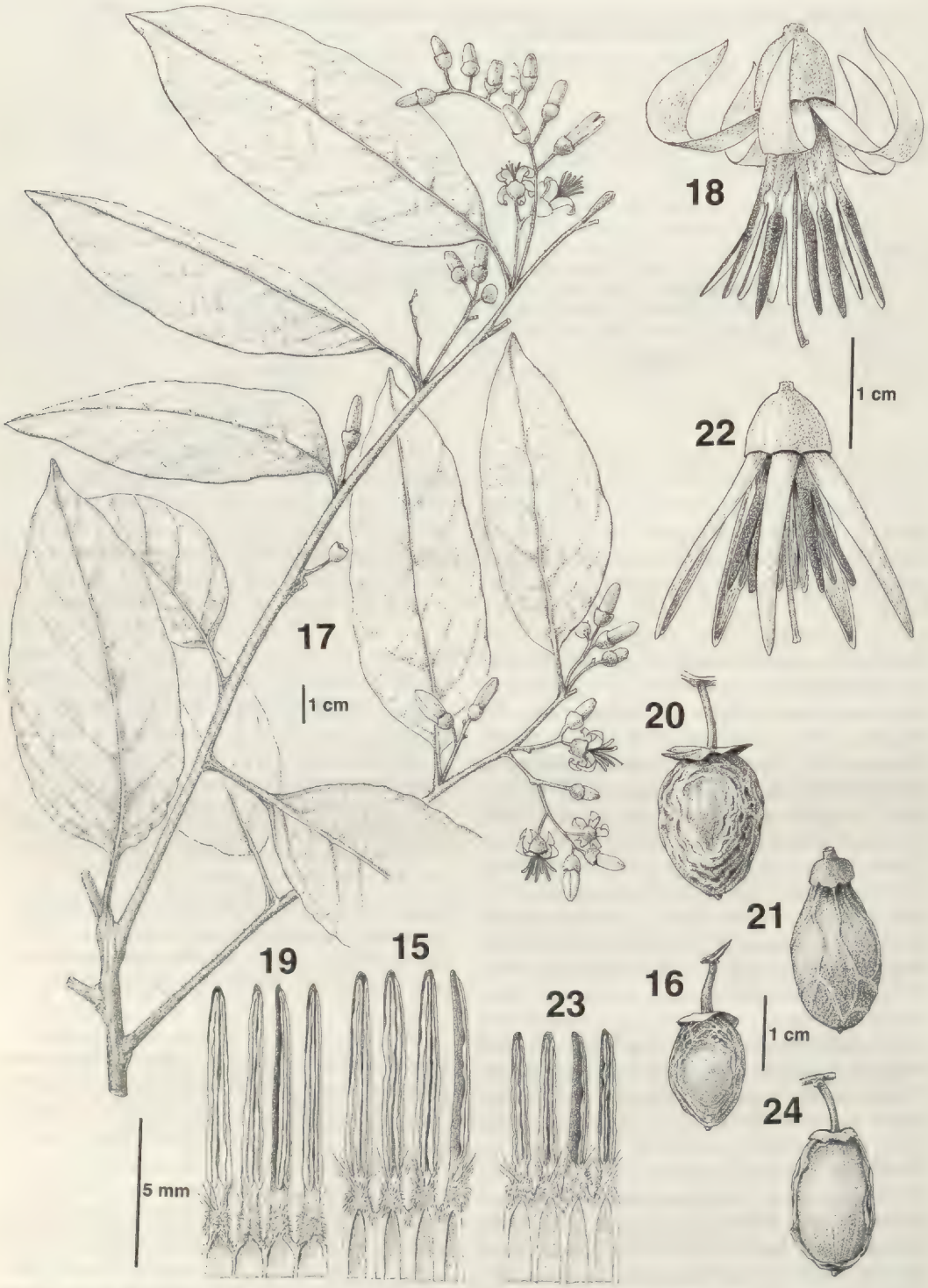
Figure 14. Distribution of *Styrax argenteus*.

secondary growth. Flowering: August–March; fruiting: October–May.

Common names. Alamo (Honduras, *Erazo 63, Standley 15947, von Hagen & von Hagen 1253*; Nicaragua, "*T-1*" *s.n.*), alomo (Honduras, *Molina & Molina 34417*), chucam-ai (Chiapas, 1919, *Becerra s.n.*), duraznillo (Guatemala, *Steyermark 51100*), estorac (El Salvador, *Standley 20147*), estoraco (Costa Rica), estoraque (El Salvador, *Calderón 1404* and *1405, Standley 20405*; Guatemala, *Morales 1208, Steyermark 50801*), estoraque común (Guatemala, *Aguilar 186* and *214*), naranjo (Guatemala, *Standley 82830*), palo blanco (Honduras, *Erazo 63, Molina 20321*), roble (Guatemala, *Steyermark 30624*), tepe aguacate (Guatemala, *Steyermark 50699*). Standley (1924) has listed additional common names for this species: bracino (Costa Rica), capulín (Oaxaca), chilacuate (Guerrero, Michoacán), estorac (El Salvador), hoja de jabón (Oaxaca), resina, resino (Costa Rica, Nicaragua), ruín (Sinaloa), and sahumerio (Panama), but because his circumscription of *S. argenteus* differs from mine, the application of these names in this revision is ambiguous. In Standley (1938) the names listed (bracino, laurel, resina, tubús; Costa Rica) are more likely to apply to *S. argenteus* as conceptualized in Standley (1924).

Uses. Fruits are sold in local markets (Chiapas, *Bauml et al. 531*); flowers are boiled with lime leaves and the water used as a perfume (Oaxaca, Dec. 1961, *MacDougall s.n.*); bark is used to poison fish (El Salvador, *Standley 20405*). Standley (1924) reported that the gum of *S. argenteus* is burned as incense in Costa Rican churches, but it is not clear whether the gum used is from *S. argenteus* as circumscribed in the present revision.

Selected specimens examined. BELIZE. **Cayo:** Río Frío Caves road, Augustine, *Meave & Howe 1162* (MO). COSTA RICA. **Alajuela:** Santiago de San Ramón-Finca Barranca, *Gómez et al. 20777* (CAS, CR, DUKE, MO). **Cartago:** Turrialba, *Córdoba 754* (CR, DUKE). **Guanacaste:** Parque Rincón de la Vieja, Hacienda Santa María, *Herrera 854* (CR, F, MO, TEX). **Heredia:** Heredia, *Williams 16067* (F, GH). **Puntarenas:** Monteverde, San Luis Valley, *Haber ex Bello 3533* (CR, DUKE, F, MO, TEX, W). **San José:** 1.4 km NW of Brazil de Santa Ana, *Taylor 17390* (F, MO, US). EL SALVADOR. **Ahuachapán:** Sierra de Apaneca, *Standley 20147* (GH, NY, US). **San Salvador:** Comasagua, *Calderón 1404* (GH, NY, US). **Santa Ana:** vicinity of Santa Ana, *Standley 20405* (GH, NY, US). GUATEMALA. **Baja Verapaz:** 10 mi. S of Rabinal, *Harmon & Dwyer 3056* (GH, MO, NY). **Chimaltenango:** along road from Chimaltenango to San Martín Jilotepeque, *Standley 57958* (F, NY). **Chiquimula:** along Tepotun River, vicinity of Esquipulas, *Molina & Molina 25328* (F, MO, US). **El Progreso:** Sierra de las Minas, 1 Jan. 1908, *Kellerman s.n.* (F). **Escuintla:** below Las Lajas, *Standley 64767* (A, F). **Guatemala:** Guatemala City, *Harmon 3461* (DS, MICH, MO, NY). **Huehuetenango:** Aguacatán, *Skutch 1935* (A, F, NY); Puente El Aguilar, just E of San Sebastián, *Standley 82830* (F, MO, US). **Jutiapa:** Quebrada above Ovejero, *Standley 77656* (F). **Quiché:** *Aguilar 758* (F). **Santa Rosa:** Volcán Tecuamburro, N of Chiquimulilla, *Steyermark 33138* (A, F). **Sololá:** Finca Belén,



Figures 15–24. 15, 16. *Styrax argenteus*. —15. Four adjacent stamens, *Palacios 34* (CAS). —16. Fruit, *Skutch 1935* (F). 17–20. *Styrax nicaraguensis* subsp. *nicaraguensis*. —17. Flowering branch. —18. Flower. —19. Four adjacent stamens. 17–19, *Webster et al. 12496* (LL). —20. Fruit, *Atwood s.n.* 8 June 1975 (MO). —21. *Styrax nicaraguensis* subsp. *ellipsoidalis*, fruit; *Dryer 1420* (F). 22–24. *Styrax steyermarkii*. —22. Flower. —23. Four adjacent stamens, *Lundell & Contreras 19214* (LL). —24. Fruit. 22, 24. *Lundell & Contreras 21219* (LL).

Lake Amatitlán, *White 5260* (F, LL, MICH, US). **Suchitepéquez:** southern lower slopes of Volcán Zunil, *Steyermark 35418* (F). **Zacapa:** between La Reforma and Teculután, *Steyermark 42075* (F, NY). HONDURAS. **Choluteca:** vicinity of San Marcos de Colón, *Standley 15875* (F). **Comayagua:** plains near Siguatepeque, *Yuncker et al. 5589* (F, GH, MICH, MO, NY, U, US). **Copán:** El Polvazal, *Ferrera 176* (NY). **El Paraíso:** near Arenar, 5 km W of Danli, *Williams & Molina 10491* (DS, F, GH, LL, MICH, MO). **Morazán:** near Cuesta Grande, *Williams & Molina 13270* (BH, F, GH, LL, MEXU, MO, US). **Tegucigalpa:** Mont. de la Flor, *von Hagen & von Hagen 1253* (F, NY). MEXICO. **Chiapas:** Intersection of Hwy. 190 and road to Tuxtla Gutiérrez airport, *Bauml et al. 531* (MICH, US); 13 km N of Arriaga along Hwy. 195, *Breedlove 28487* (DS, DUKE, F, LL, MEXU, MICH, MO, NY, RSA); El Zapotal, al SE de Tuxtla Gutiérrez, *Palacios 34* (CAS). **Guerrero:** La Providencia, Mar. 1926, *Ferris s.n.* (DS). **Oaxaca:** between Trapiche Santa Ana and T. del Lazo, *Conzatti 4558* (NY, US); San Bartolo Yautepec, Dec. 1961, *MagDougall s.n.* (MEXU). NICARAGUA. **Boaco:** Cerro Mombachito, *Aranda et al. 40* (MO, NY). **Chontales:** ca. 2.8 km above (N of) Cuapa, *Stevens 22709* (MO). **Estelí:** Paso de León, 3.5 km al NW de Estelí, *Moreno 10854* (DUKE, MEXU, MO, NY). **Madriz:** Cerro El Fraile, *Moreno 23512* (MEXU, MO). PANAMA. **Coclé:** vicinity of Olá, *Pittier 5076* (GH, NY, US).

Styrax argenteus is one of the most common species of *Styrax* in the area circumscribed by this revision. It is distinguished from sympatric species by its evergreen leaves, grayish green stellate pubescence on the lower laminar surface and calyx (i.e., no orange-brown hairs), corolla lobes united up to the calyx margin, and slightly auriculate stamen filaments bearing long-armed and relatively stiff stellate hairs ventrally; the hairs nearest the distal end of the filament possess the longest arms, which predominantly point upward. It is a relatively low-elevation species, unlike most other *Styrax* species in the region. Generally this species does not extend lower than 400 m, but it does occur at or below 100 m in Guanacaste Province, Costa Rica (OTS Research Area A, *Frankie 239a*) and Coclé Province, Panama (*Pittier 5076*).

The differences between *S. argenteus* and *S. nicaraguensis* are subtle. *Styrax nicaraguensis* has orange-brown hairs on the calyx and the lower laminar surface, a larger drupe, a highly restricted range, and a different habitat. Sterile specimens of *S. argenteus* are difficult to distinguish from the equally common *S. warscewiczii*: *S. argenteus* tends to have larger leaves that are fulvescent when young, and often has longer, relatively loose and soft hairs abaxially. However, some sterile specimens cannot be determined, particularly those from saplings or stump sprouts, or from undocumented elevations and/or habitats.

My treatment of *S. argenteus* differs from those of Perkins (1907) and Gonsoulin (1974). I agree with Gonsoulin (1974) that *S. argenteus* was unnecessarily divided into several species by Perkins (1902). *Styrax myristicifolius* and *S. polyanthus* both fall within the range of variation encompassed by my concept of *S. argenteus* [Perkins later (1907) placed *S. myristicifolius* in synonymy under *S. argenteus*]. However, I strongly disagree with Gonsoulin's (1974) revised concept of *S. argenteus*. This concept includes not only the clearly distinct species *S. magnus, S. ramirezii,* and *S. warscewiczii,* all of which were described prior to Gonsoulin's revision, but also the species now recognized as *S. austromexicanus, S. radians,* and *S. steyermarkii.* Gonsoulin annotated specimens of the latter three species as *S. argenteus* despite examining material with diagnostic characters. He also annotated the type of *S. panamensis* as *S. argenteus* but failed to include this name in the treatment.

To account for the high amount of variation present in his circumscription, Gonsoulin (1974) recognized two varieties of *Styrax argenteus* in addition to the typical variety: variety *hintonii* and variety *ramirezii* (= var. *micranthus*). The three varieties were distinguished by the type and amount of pubescence on the lower laminar surface and the calyx, but essentially exhibited no ecological or geographic distinctions. Although calyx hair types are critical characters in the delimitation of *Styrax* species, the hairs on the lower laminar surface tend to be more variable and unreliable. When Gonsoulin attempted to reconcile the relatively constant nature of the calyx pubescence with the variable nature of the leaf pubescence, the result was the recognition of a large number of intermediates throughout the ranges of the varieties. For example, *S. argenteus* var. *ramirezii* is distinguished from variety *argenteus* by a thin versus thick tomentum on the lower laminar surface. However, *S. argenteus* in my view is polymorphic for this character in that individuals always possess the thin tomentum, but in addition often have an additional layer of longer hairs. The majority of specimens examined by Gonsoulin that are assigned here to *S. argenteus* were annotated by him as variety *argenteus,* primarily because *S. argenteus* usually possesses the longer hairs. However, a considerable portion were annotated as variety *ramirezii* (those with the long pubescence absent), or intermediates between this and the typical variety. When the hairs are unusually long, specimens of *S. argenteus* were annotated by Gonsoulin as variety *hintonii* or as a variety *hintonii* intermediate (it is never stated what the second taxon is in cases of purported intermediacy). The high number of intermediates assigned to variety *argenteus* and variety *ramirezii* by Gonsoulin

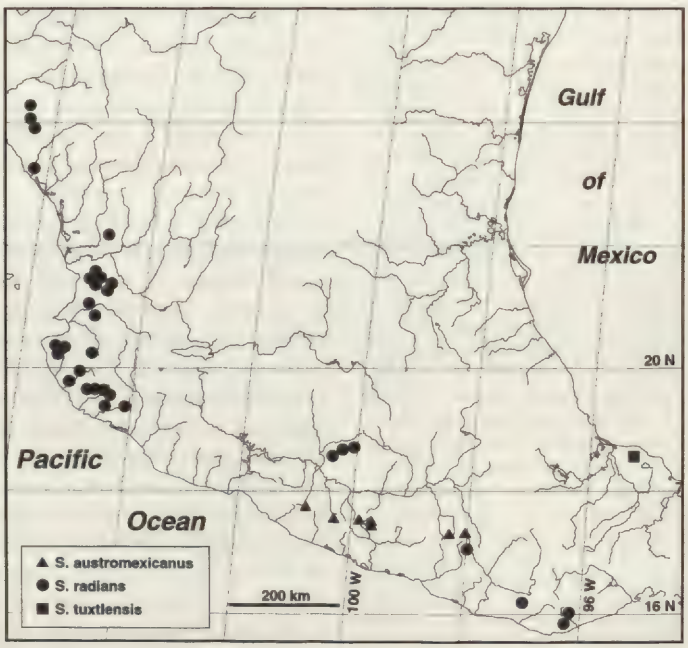


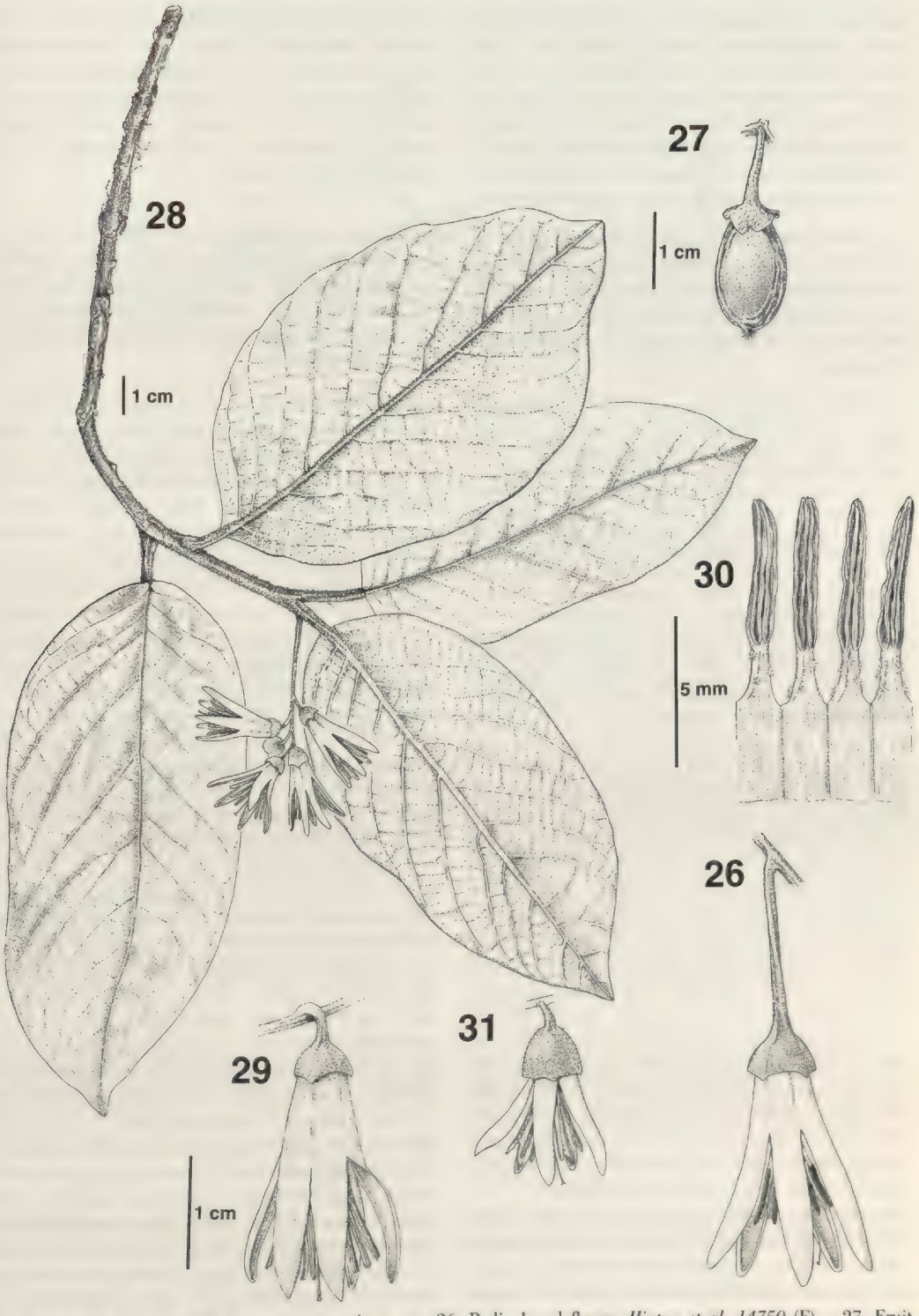
Figure 25. Distribution of *Styrax austromexicanus*, *S. radians* and *S. tuxtlensis*.

is accounted for to a large extent by the variable amount of the longer hairs present in individuals of *S. argenteus*. In the present treatment *S. argenteus* vars. *ramirezii* and *hintonii* are synonyms of *S. ramirezii*.

The collection date of the type of *S. argenteus* is probably October–December 1791 (McKelvey, 1955).

2. Styrax austromexicanus P. W. Fritsch, nom. et stat. nov. Based on: *Styrax argenteus* var. *grandiflorus* E. Carranza, Acta Bot. Mex. 36: 15. 1996, non *S. grandiflorus* Griff., 1854. TYPE: Mexico. Oaxaca: Mpio. de Juxtlahuaca, 3 km S of the road to San Martín Peras on the road to Coicoyán de Las Flores, 27 Sep. 1993, *J. L. Panero et al. 3475* (holotype, MEXU not seen; isotypes, ENCB not seen, IEB not seen, MSC). Figures 25–27.

Evergreen tree to 17 m. Young twigs predominantly and densely orange-brown-stellate-pubescent or -villous, with intermixed scattered short-armed white stellate hairs; outer layer of older twigs not exfoliating. Petiole 13–21 mm long. Lamina thick-chartaceous, 11–18 × 3.5–5 cm, usually narrowly elliptic, sometimes slightly oblanceolate, slightly ovate, or elliptic, secondary veins about 13; apex acute to abruptly acuminate; base cuneate to subrounded, symmetric or slightly oblique; adaxially glabrous except along the major veins or rarely sparsely stellate-pubescent; abaxially covered with minute whitish stellate hairs, larger whitish hairs and evenly scattered orange-brown hairs, the three types occurring on the secondary and tertiary veins, thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, racemes or panicle branches 3.5–6.5 cm long, 2–11-flowered. Lower pedicels 11–15 mm long. Calyx 4–5 × 5–6 mm, conical or broadly cupuliform, light grayish green-stellate-pubescent, with a variable amount of larger orange-brown stellate hairs; calyx teeth 5, to 0.5 mm long, deltoid or more often indistinct from the calyx margin, rarely absent, calyx margin truncate or more often slightly concave between the teeth, inner margin rarely glandular. Corolla pink or white, 14–23 mm long, petals connate 2–5 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 8–17 × 2.5–3.5 mm, non-overlapping, erect or spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 3.5–6 mm long; distinct portion of filament 1.5–2 mm long, of equal width throughout, ventrally not auriculate, sparsely white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.5 mm long; anthers 4.5–5.2



Figures 26–31. 26, 27. *Styrax austromexicanus.* —26. Pedicel and flower, *Hinton et al. 14750* (F) —27. Fruit, *Rzedowski 18529* (TEX). 28–30. *Styrax incarnatus, Lundell & Contreras 19618* (LL). —28. Flowering branch. —29. Pedicel and flower. —30. Four adjacent stamens. —31. *Styrax lanceolatus,* pedicel and flower; *Johnston 7408* (TEX).

mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style pubescent from base to 45–90% of the total length; stigma 0.3–0.5 mm wide. Drupe 17–19 × 10–12 mm, obovoid, slightly beaked by the base of the persistent style; wall irregularly and coarsely rugose on herbarium specimens. Seed coat sparsely white-stellate-pubescent.

Guerrero and western Oaxaca, Mexico, in the Sierra Madre del Sur; bosque mesofilo de montaña, *Quercus-Pinus-Abies* forest; 2100–3000 m; found in rocky limestone areas. Flowering: June, September, October; fruiting: February, April, June, September, November.

Additional specimens examined. MEXICO. **Guerrero:** 16 km SW of Filo de Caballo, *Breedlove & Almeda 64929* (CAS); W of Puerto El Gallo along road to Toro Muerto, *Breedlove & Almeda 65176* (CAS); 4 km del Carrizal de Bravos, *Fonseca 163* (MEXU); Dto. de Galeana, Piedra Ancha, *Hinton et al. 14750* (F, GH, LL, MO, NY, US); 11 km al SW de Filo de Caballo, *Martínez et al. 4906* (F, LL, MEXU); Mpio. de Coyuca de Catalán, Cerro del Chivo, *Medrano et al. 6706* (GH, MEXU); Puerto Chico, 10 km al W de Camotla, *Rzedowski 18529* (MEXU, MICH, RSA, TEX); 6 km al NW de Omiltemi, *Tenorio et al. 2642* (MO); Mpio. de Chilpancingo, entre los cerros de la Aguililla y Plan de Potrerillos, *Valdez 616* (MEXU). **Oaxaca:** E de Xatu Yahta, al W Coicoyán, *Avila 742* (CAS); km 18 on the road to Cañada de Lobos, Gorge of the Río Ratón, *Panero 5254* (MSC).

Styrax austromexicanus is a rare endemic to the cloud forests of the Sierra Madre del Sur in Guerrero and Oaxaca, Mexico. Except for *S. incarnatus*, it has the largest flowers of any evergreen *Styrax* species in the region. It can be distinguished from sympatric species by its stellate pubescence throughout, narrowly elliptic evergreen leaves, mixture of white and orange-brown hairs on the lower laminar surface and calyx, large, usually pink flowers with a long corolla tube, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. In addition, the secondary and tertiary veins of the lower laminar surface are obscured by the tomentum, distinguishing this species from most specimens of *S. ramirezii*. This species appears to be allied to *S. incarnatus* of Guatemala and Honduras, from which it differs principally by its narrowly elliptic leaves.

As the first known specimen of this species was not collected until 1939 (*Hinton 14750*), Perkins did not see this species. Gonsoulin (1974) annotated both collections he examined as *Styrax argenteus* var. *argenteus*, and Carranza (1996) also considered this species to be a variety of *S. argenteus* (var. *grandiflorus*). However, in contrast to *S. argenteus* as circumscribed here, *S. austromexicanus* possesses white or pink (vs. consistently white) flowers, non-tapered anther sacs, non-prolonged anther connectives, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. I consider the sum of these character differences to justify recognition of this taxon at the species level.

3. Styrax conterminus Donn. Sm., Bot. Gaz. 18: 5. 1893. TYPE: Guatemala. Quiché: San Miguel Uspantán, Apr. 1892, *Heyde & Lux 2915* (holotype, US; isotypes, B destroyed, GH, HRCB not seen, M not seen, MO, NY). Figures 7, 32–35.

Evergreen tree to 18 m. Young twigs lepidote, the scales brown mixed with olive-green; outer layer of older twigs not exfoliating. Petiole 13–25 mm long. Lamina thick-chartaceous, 8.5–16.5 × 2.7–5.0 cm, 2.8–3.9 times as long as wide, narrowly elliptic or narrowly oblong, secondary veins 11–13; apex acuminate; base cuneate to slightly attenuate, symmetric or slightly oblique; adaxially glabrous or sparsely lepidote; abaxially covered (surface and veins) with olive-green peltate or lacerate-margined scales, and more scattered orange-brown scales; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, racemes or panicle branches 3–5.5 cm long, 4–9-flowered. Lower pedicels 8–12 mm long. Calyx 3–4 × 4–5.5 mm, conical, olive-green-, light brown-, or orange-brown-lepidote, scales at mid-calyx 0.33–0.42 mm diam., peltate or lacerate-margined; calyx teeth 5, to 0.7 mm long, deltoid; calyx margin slightly concave or rarely truncate between the teeth, inner margin rarely glandular. Corolla white or pink, 10–13 mm long, petals connate 2–4 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 7–10 × 3 mm, non-overlapping, erect or spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of peltate or lacerate-margined scales. Free portion of stamen tube 2–3 mm long; distinct portion of filament 1–2 mm long, of equal width throughout, ventrally not auriculate, sparsely radiate-lepidote at the somewhat incurved filament margins, glabrous on the face, the scales with arms to 0.4 mm long; anthers 3.5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary lepidote; style glabrous or pubescent at base only; stigma 0.4–0.5(–0.8) mm wide. Drupe 12–15 × 7–9 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

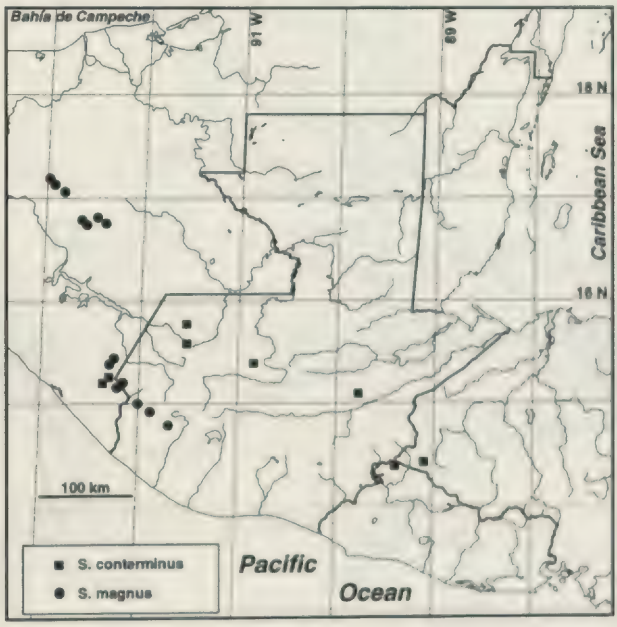


Figure 32. Distribution of *Styrax conterminus* and *S. magnus*.

Southern Chiapas to western Honduras and northern El Salvador; ± 1500–2800 m; *Pinus-Quercus-Ostrya* forest, broad-leaved cloud forest. Flowering: April–June, December; fruiting: January, February, June, August.

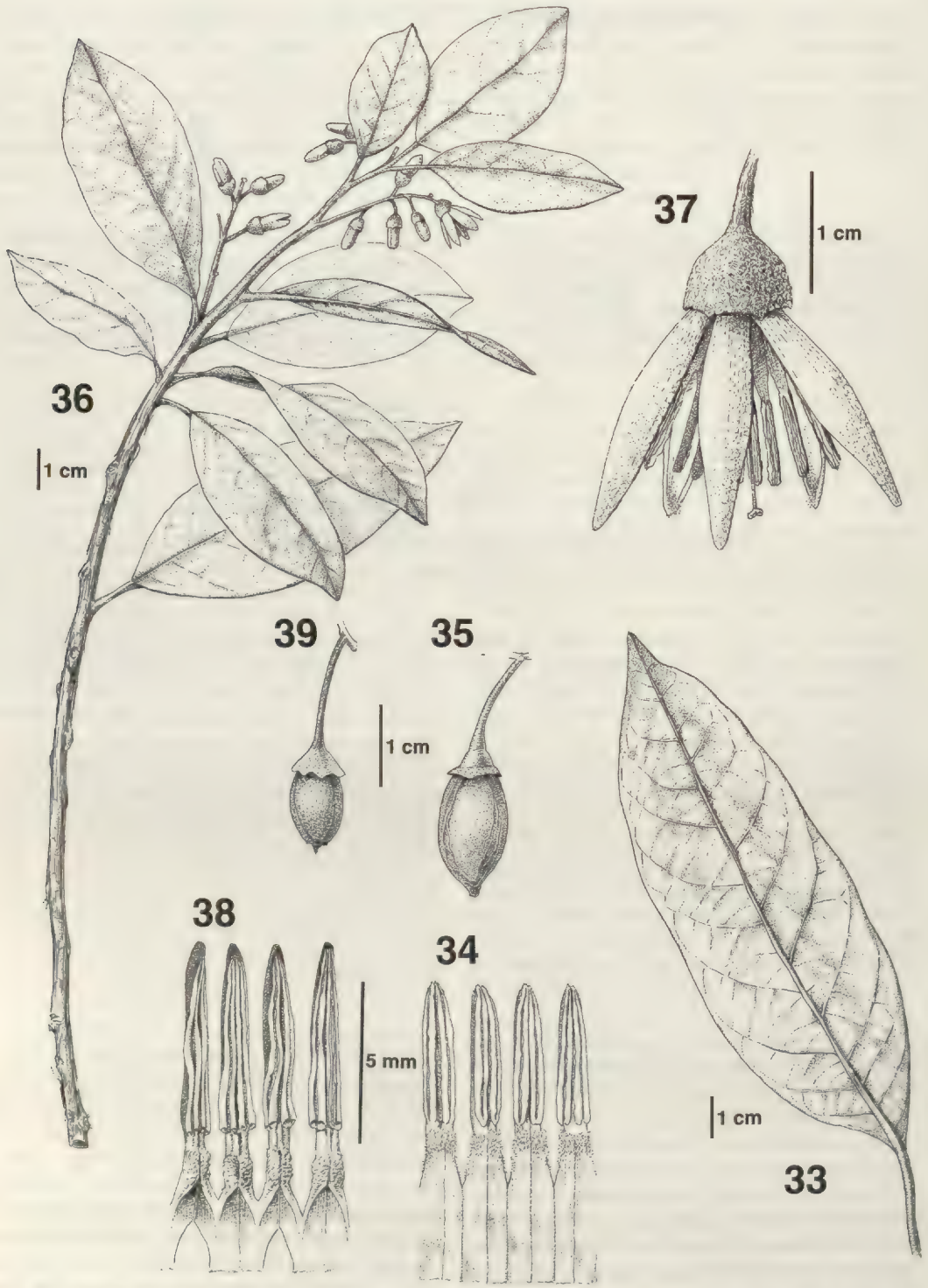
Common names. Copalillo (El Salvador, 4 June 1976, *Reyna s.n. p.p.*).

Additional specimens examined. EL SALVADOR. **Santa Ana:** Cerro Montecristo, *Allen 7184* (F, GH, LL, MICH, US), 4 June 1976, *Reyna s.n. p.p.* (CR). GUATEMALA. **Huehuetenango:** above Puente Alto, *Sharp 45107* (*451047*) (F, GH, MEXU, MO, NY); above San Juan Ixcoy, Sierra de los Cuchumatanes, *Stevermark 49982* (F, US). **Zacapa:** slopes of Volcán Gemelos, *Steyermark 43279* (A, F, NY). HONDURAS. **Ocotepeque:** Alrededor de la Laguna Verde, 12 km al SE de Nueva Ocotepeque, *Darío 59* (DUKE). MEXICO. **Chiapas:** on ridge NE of Cerro Boquerón on road from El Rosario to Niquivil, *Breedlove 68928* (CAS); Niquivil, near Motozintla, *Matuda 15507* (CAS, F, LL, NY); Cerro del Boquerón, *Purpus 7422* (GH, NY).

Styrax conterminus is a rare endemic to northern Mesoamerica. It is easily distinguished from other species within its range by the possession of peltate or lacerate-margined scales on the leaves, twigs, and inflorescences. The only other species in the region with this feature is *S. peruvianus*, which can be distinguished by its auriculate stamen filaments and proportionally broader leaves.

This species possesses an unusual combination of character states. The presence of peltate scales is a feature shared with *Styrax peruvianus* and other South American species, e.g., *S. cordatus* (Ruiz & Pav.) A. DC. [likely = *S. ovatus* (Ruiz & Pav.) A. DC.] and *S. leprosus* Hook. & Arn. and is clearly derived within the genus. These species possess other putative derived characters, such as auriculate stamen filaments and tapered anther sacs, whereas *S. conterminus* has non-auriculate stamen filaments and non-tapered anther sacs (polarity as determined from the outgroup taxa *Pamphilia* and *S. foveolaria*). Many other South American species (e.g., *S. guianensis* A. DC., *S. subargenteus* Sleumer) have stellate-pubescent calyces but tapered anther sacs and/or auriculate stamen filaments. This combination of characters in *S. conterminus* suggests three possible evolutionary pathways for this species: (1) derivation from a peltate-scaled ancestor followed by multiple losses of auriculate stamen filaments and tapered anther sacs; (2) derivation from a non-auriculate ancestor followed by convergent evolution of peltate scales; (3) speciation resulting from hybridization involving a non-auriculate, stellate-pubescent taxon and a peltate-scaled, auriculate taxon, whereby non-auriculate anthers, non-tapered anther sacs, and peltate scales were fixed in the hybrid species. Detailed phylogenetic analysis using morphological and molecular characters would help to determine the likelihood of each of these possibilities.

The protologue of *Styrax conterminus* does not specify the holotype location. Gonsoulin (1974) in-



Figures 33–39. 33–35. *Styrax conterminus*. —33. Leaf. —34. Four adjacent stamens. 33, 34, *Sharp 45107* (= *451047*; F). —35. Fruit, *Allen 7184* (MICH). 36–39. *Styrax peruvianus*. —36. Flowering branch. —37. Flower. —38. Four adjacent stamens. 36–38, *Croat 37190* (MO). —39. Fruit, *I INBio 16* (MO).

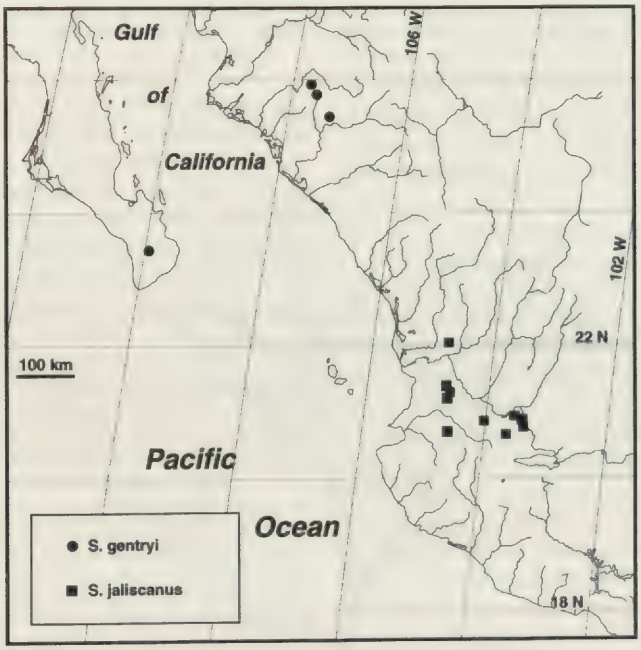


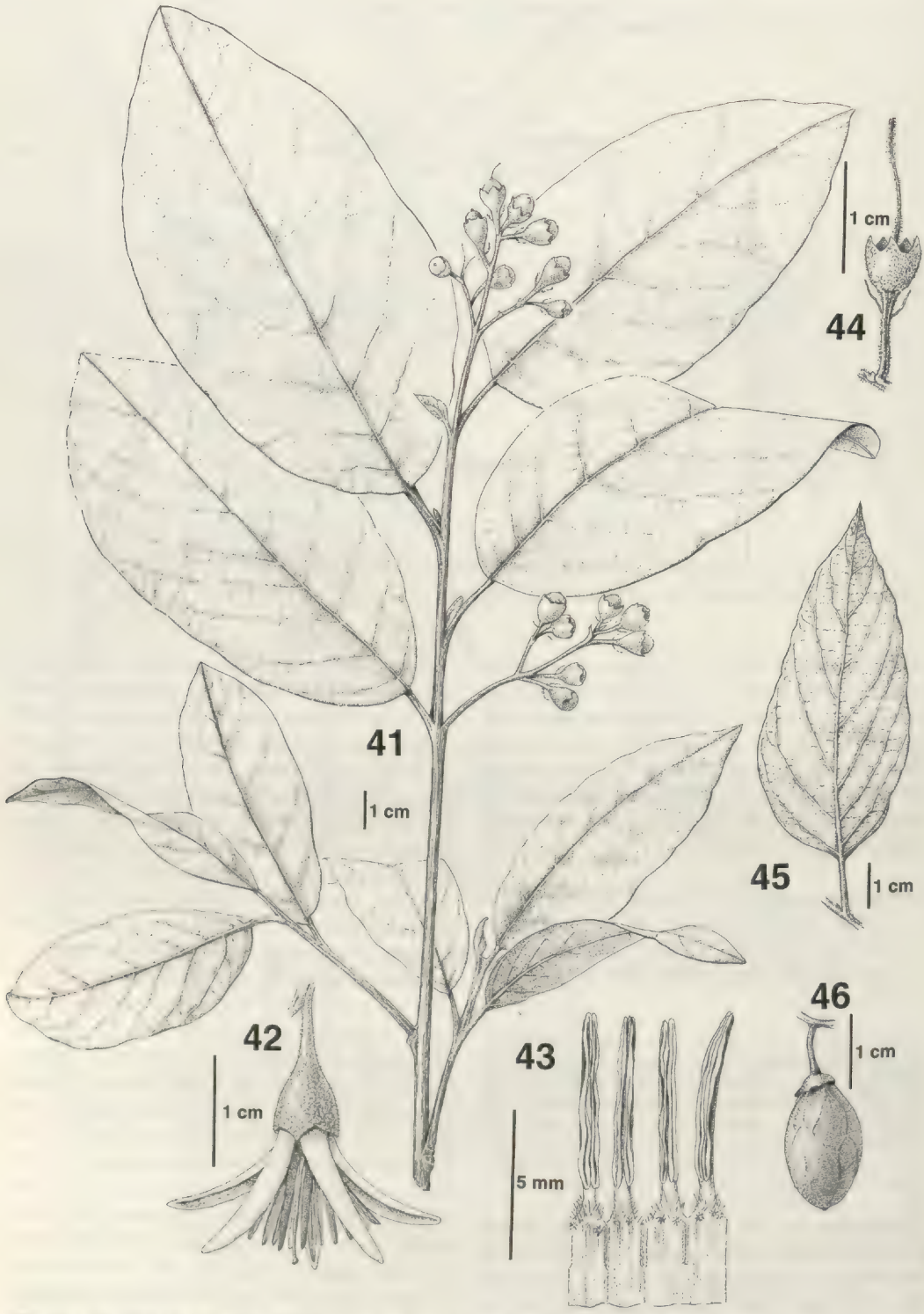
Figure 40. Distribution of *Styrax gentryi* and *S. jaliscanus*.

dicated that the holotype of *S. conterminus* was deposited at MO. However, the label heading of the type collection states "Ex plantis guatemalensibus, quas edidit John Donnell Smith," and John Donnell Smith donated his herbarium to US. If the collection originated from Donnell Smith's herbarium, as seems likely, then the holotype is best considered to be at US rather than MO.

4. Styrax gentryi P. W. Fritsch, sp. nov. TYPE: Mexico. Sinaloa: Ocurahui, Sierra Surotato, 1–10 Sep. 1941, *H. S. Gentry 6244* (holotype, DS; isotypes, GH, MICH, MO, NY). Figures 40–44.

Arbor sempervirens; *lamina* subtus alba-stellata-pubescens; *calyx* dentibus 1–2 mm longis, contiguis; *corolla* lobis in aestivatione valvatis, sub anthesi apertis; *filamenta* staminum partibus distinctis ad margines ventrales pilis stellatis aequiliter dispersis instructa, aliter fere glabra ventraliter praeter ad apices, brachis pilorum plus minusve radiatis ex axibus centralibus; *connectivum* antherae loculos non-contractos non vel leviter superans.

Evergreen tree to 17 m. Young twigs grayish green-stellate-pubescent mixed with scattered orange-brown stellate hairs; outer layer of older twigs not exfoliating. Petiole 11–18 mm long. Lamina chartaceous, 13–18 × 6–8 cm, ovate, broadly elliptic, or slightly oblanceolate, secondary veins 16–20; apex acuminate to abruptly acuminate; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute greenish white stellate hairs and more scattered larger greenish white stellate hairs, both types almost always covering the secondary and tertiary veins, thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 3–6.5 cm long, 2–7-flowered. Lower pedicels 6 mm long. Calyx 6–8 × 5–7 mm, campanulate, whitish green-stellate-pubescent; calyx teeth 5, 1–2 mm long, deltoid, contiguous, inner margin often glandular. Corolla of unknown color, 17–20 mm long, petals usually connate 3 mm beyond the calyx margin distally; corolla lobes 5, presumably valvate in bud, 15 × 2 mm, non-overlapping, spreading or recurved, thickened, linear, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 4 mm long; distinct portion of filament 1.0–1.4 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face, the hairs with arms to 0.4 mm long; anthers 6 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3 mm wide. Largest drupe observed (only immature fruits available for study) 10 × 7 mm, ellipsoid; wall ir-



Figures 41–46. 41–44. *Styrax gentryi*. —41. Fruiting branch, *Gentry 6244* (vegetative; MO) and *Breedlove 15588* (infructescence; F). —42. Flower. —43. Four adjacent stamens. 42, 43, *Domínguez 28* (HCIB). —44. Calyx. *Gentry 6244* (MO). 45, 46. *Styrax tuxtlensis*. —45. Leaf, *LaFrankie 1306* (CAS). —46. Fruit, *LaFrankie 1306* (MO).

regularly and coarsely rugose on herbarium specimens. Seed coat observed immature, glabrous.

Sierra de La Laguna, Baja California Sur and Sierra Surotato, Sinaloa, Mexico; 1600–2200 m; *Quercus-Pinus* forest, mixed dominants forest; found in riparian situations, such as arroyos, steep moist ravines, and deep rocky canyon bottoms. Flowering: October, probably also in March, August; fruiting: March, October

Common name. Aguacatillo (Baja California Sur, *Domínguez 28*).

Additional specimens examined. MEXICO. **Baja California Sur:** Sierra de la Laguna, Arroyo de los Encinos Blancos, *Domínguez 28 ("R.D.C.")* (HCIB); Sierra de la Laguna, *Gentry 4420* (DS, GH, MO). **Sinaloa:** Sierra Surotato, near Los Ornos, *Boutin & Brandt 2878* (CAS), *Breedlove 15588* (CAS, F, NY); Sierra Surotato, Mpio. de Badiraguato, Ocurahui valley, *Breedlove & Kawahara 16893* (CAS); Sierra Surotato, 5 mi. NW of Los Ornos, *Breedlove & Thorne 18269* (CAS, RSA); Sierra Surotato, 3 mi. N of Los Ornos, *Breedlove & Thorne 18414* (CAS); Sierra Surotato, 5 mi. NE of La Ciénega, *Breedlove & Thorne 18584* (CAS, RSA).

Styrax gentryi is a rare species with a disjunct distribution in the Sierra de la Laguna of Baja California's Cape Region and the Sierra Surotato in northwestern Sinaloa, Mexico. It is particularly appropriate that the species be named after Howard Scott Gentry (1903–1993), considering that he was able to collect this plant in both disjunct localities—from Baja California Sur in 1939 (the first collection of the species) and Sinaloa in 1941.

This species is easily distinguished from all other species of evergreen *Styrax* by the prominent calyx teeth, evident even in fruit. This is one feature that probably led Gonsoulin (1974) to include *Gentry 6244* and *Gentry 4420* within the deciduous capsular-fruited species *S. jaliscanus*. These collections were made just after anthesis, so no flowers or fruits are available for examination. However, a third collection (*Breedlove 15588*) with the same calyces and leaves as the Gentry collections is annotated as *S. argenteus* var. *argenteus* by Gonsoulin. This collection has immature fruit that establishes its affinity with the evergreen, drupe-bearing species rather than the deciduous, capsule-bearing species. A relatively recent flowering collection (*Domínguez 28*) further confirms the affinity of this species with the evergreen taxa by virtue of its non-overlapping corolla lobes.

This species's disjunct distribution seems not to be strictly paralleled in other flowering plants, although distribution patterns of at least two species are similar: *Populus monticola* Brandegee and *Ilex tolucana* Hemsl. both occur in the Sierra de la Laguna of the Cape Region of Baja California Sur and in the same habitat as *Styrax gentryi*. However, on the mainland, *P. monticola* occurs in Sonora, and *I. tolucana* is disjunct from Sonora to Veracruz and Oaxaca (L. Lenz, pers. comm.). Additional collections contributing to the still poorly known flora of Sinaloa may reveal more taxa that are disjunct from the Sierra Surotato and the Sierra de la Laguna.

The Cape Region first split from northern Jalisco in the mid-Miocene (13–14 Mya; Smith, 1991) and existed as an island until the establishment of the Isthmus of La Paz in the Pleistocene (López Ramos, 1983; Fenby & Gastil, 1991). Because the two areas circumscribed by the range of *S. gentryi* were never directly connected, explaining this disjunction by vicariance would require a prior mainland distribution that extended at least partly into Nayarit and Jalisco. Although the narrow range of this species in the two disjunct areas suggests relictual status, *S. gentryi* is presumably bird-dispersed and the current mainland distribution does not extend south of northern Sinaloa. Thus, dispersal across the Gulf of California remains a viable explanation. Genetic analysis of disjunct populations of *S. gentryi* and additional information regarding its distribution and ecology would help to clarify this biogeographic issue.

5. Styrax glabratus Schott, in Spreng., Syst. veg. 4(2): 406. 1827. *Strigilia glabrata* (Schott) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 283. 1859. TYPE: Brazil. Rio de Janeiro: *Sellow 807* (holotype, ?BP; isotypes, F, US (2)). Figure 47.

Styrax erymophyllus Pohl ["*S. erymophyllum*"]. Pl. bras. icon. descr. 2: 57. 1830. TYPE: Brazil. Rio de Janeiro: *Schott 4184* (holotype, W; isotypes, BR(2), F, GH, W(3)).

Epigenia integerrima Vell., Fl. flumin. 183. 1829. TYPE: Icon. 4, t. 137 in Vell., Fl. flumin., 1831 (holotype).

Styrax psilophyllus A. DC., Prodr. 8: 266. 1844 ["*S. psilophyllum*"]. *Strigilia psilophylla* (A. DC.) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 283. 1859. TYPE: French Guiana. Cayenne, *Martin s.n.* (holotype, P; isotype, US).

Styrax leiophyllus Miers. in Lindl., Veg. kingd. Ed. 3: 593a, t. 402 p.p. 1853 ["*S. leiophyllum*"]. *Strigilia leiophylla* (Miers) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 283. 1859. TYPE: Brazil. Rio de Janeiro: Valença, *John 1345* (holotype, BM not seen; photo of holotype, NY).

Styrax lauraceus Perkins, Bot. Jahrb. Syst. 31: 478. 1902. TYPE: Venezuela. Distrito Federal: Galipan, *Karsten 41* (holotype, B destroyed; photo of holotype, NY(2); isotype, F).

Styrax squamulosus M. F. Silva, Acta Amazon. 1: 23. 1971 ["*S. squamulosa*"]. TYPE: Brazil. Amazonas: Manaus, Reserva Florestal Ducke, 1390 Levantamento,

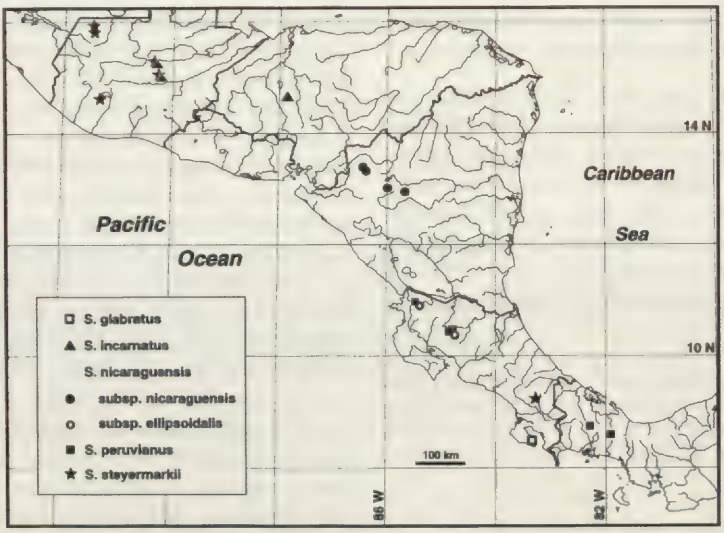


Figure 47. Distribution of *Styrax glabratus, S. incarnatus, S. nicaraguensis* subsp. *nicaraguensis, S. nicaraguensis* subsp. *ellipsoidalis, S. peruvianus,* and *S. steyermarkii.*

14 Mar. 1971, *W. Rodrigues & D. Coêlho 8342* (holotype, INPA not seen; isotype, NY).

Evergreen tree to 20 m. Young twigs sparsely to densely greenish gray-stellate-pubescent or radiate-lepidote; outer layer of older twigs not exfoliating. Petiole 5–16 mm long. Lamina subchartaceous, 9–19 × 2.5–6 cm, 2.2–3.8(–5.2) times as long as wide, elliptic or oblanceolate, secondary veins 6–9; apex acute to acuminate; base cuneate, symmetric or slightly oblique; adaxially glabrous or sparsely pubescent on the midvein at the base; abaxially glabrous except for the midvein at the base, or rarely sparsely stellate-pubescent or radiate-lepidote, occasionally with domatia in the axils of the secondary veins, the hairs white to grayish green; margin entire. Inflorescences axillary or false-terminal, racemose or rarely paniculate, the racemes or panicle branches 2–7 cm long, (1)2–8-flowered. Lower pedicels 2–13 mm long. Calyx 4–7 × 4–6 mm, cupuliform, usually grayish green-radiate-lepidote (always in Costa Rica), sometimes with a few orange-brown radiate scales toward the base, rarely (SE Brazil) stellate pubescent; scales at mid-calyx 0.13–0.29 mm diam.; calyx teeth 5 or often absent, to 0.5 mm long, linear-deltoid, the calyx margin truncate between the teeth, inner margin eglandular. Corolla white to pale pink, 13–20 mm long, petals connate 1–4 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 8–13 × 2.5–3 mm, non-overlapping, reflexed, slightly thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of radiate scales or stellate hairs. Free portion of stamen tube 2–2.5 mm long; distinct portion of filament 1.5–2 mm long, somewhat incurved, of equal width throughout, ventrally not auriculate, each margin with a cluster or longitudinal line of stiff white stellate hairs, these sometimes also occurring on the ventral face, the hairs with arms to 1.8 mm long, the hairs nearest the distal end of the filament with arms predominantly directed upward; anthers 5–8 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely short-stellate-pubescent; style glabrous; stigma 0.3–0.4 mm wide. Drupe 13–18 × 7–9 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens; fruiting calyx funnelform, 4–8 mm long. Seed coat glabrous.

Osa Peninsula, SW Costa Rica; also Colombia, Venezuela, Suriname, French Guiana, and Brazil; 400 m in Costa Rica. Flowering: October (buds) in Costa Rica.

Specimens examined. COSTA RICA. **Puntarenas:** Cantón de Golfito Jiménez, Río Piro camino a Cerro Osa, *Herrera 4534* (CR, INB).

In North America, *Styrax glabratus* has thus far been documented only from the Osa Peninsula in Costa Rica; the major portion of its range is in South America, from Colombia to southeastern Brazil. The existence on the Osa Peninsula of a species otherwise found only in South America is not discordant with the general composition of the Osa flora, which comprises many endemics and species otherwise not known in Costa Rica and has strong affinities to the flora of the Chocó region in Colom-

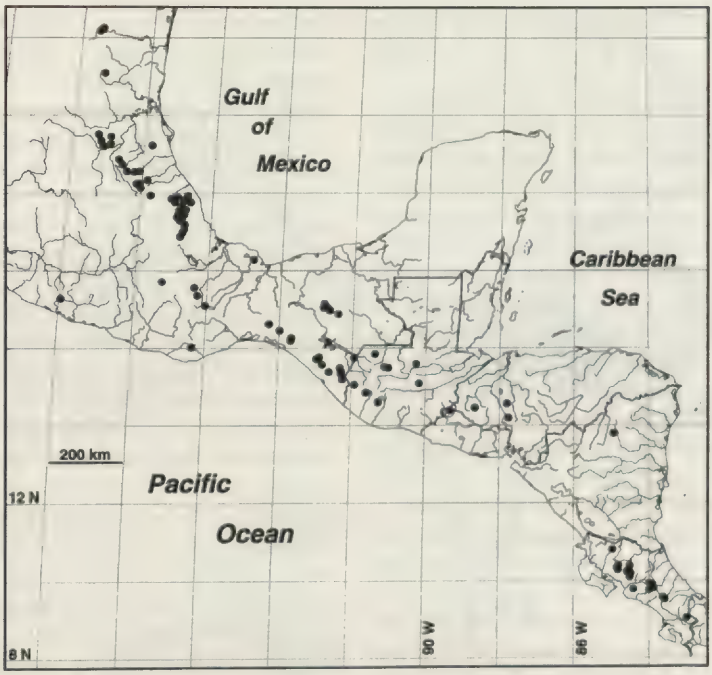


Figure 48. Distribution of *Styrax glabrescens.*

bia (Hartshorn, 1983; Grayum & de Nevers, 1988). In South America, the species is most commonly found close to the margins of the continent in restingas, pluvial forests, and moist evergreen forests, but in northern South America it extends as far inland as Manaus, Brazil, where it occurs in terra firme forests on clay.

The species is easily distinguished from other species in Costa Rica by its evergreen habit, glabrous abaxial laminar surface, and drupaceous fruit. The lamina of *Styrax glabrescens* is also nearly to completely glabrous abaxially and adaxially, but that species is deciduous and has a dry fruit. Rarely *S. warscewiczii* has nearly glabrous abaxial laminar surfaces as well, but it has smaller leaves, usually occurs above 1500 m elevation, and the ventral side of the stamen filaments has hairs with short arms (to 0.3 mm long).

In Espirito Santo and extreme southern Bahia, Brazil, the calyx of *S. glabratus* is stellate-pubescent, not radiate-lepidote as is otherwise the case. Plants of *S. glabratus* with this feature will key to *S. argenteus* in the present treatment. *Styrax argenteus* can be distinguished from *S. glabratus* by the possession of densely stellate-pubescent abaxial leaf surfaces and the presence of small auricles partly hidden by the hair mass at the margins of the stamen filaments; the leaf of *S. glabratus* is glabrous or nearly so on both sides and the stamen filaments lack auricles.

An additional collection from the Osa Peninsula (*Aguilar 4140*) is also reportedly *S. glabratus.*

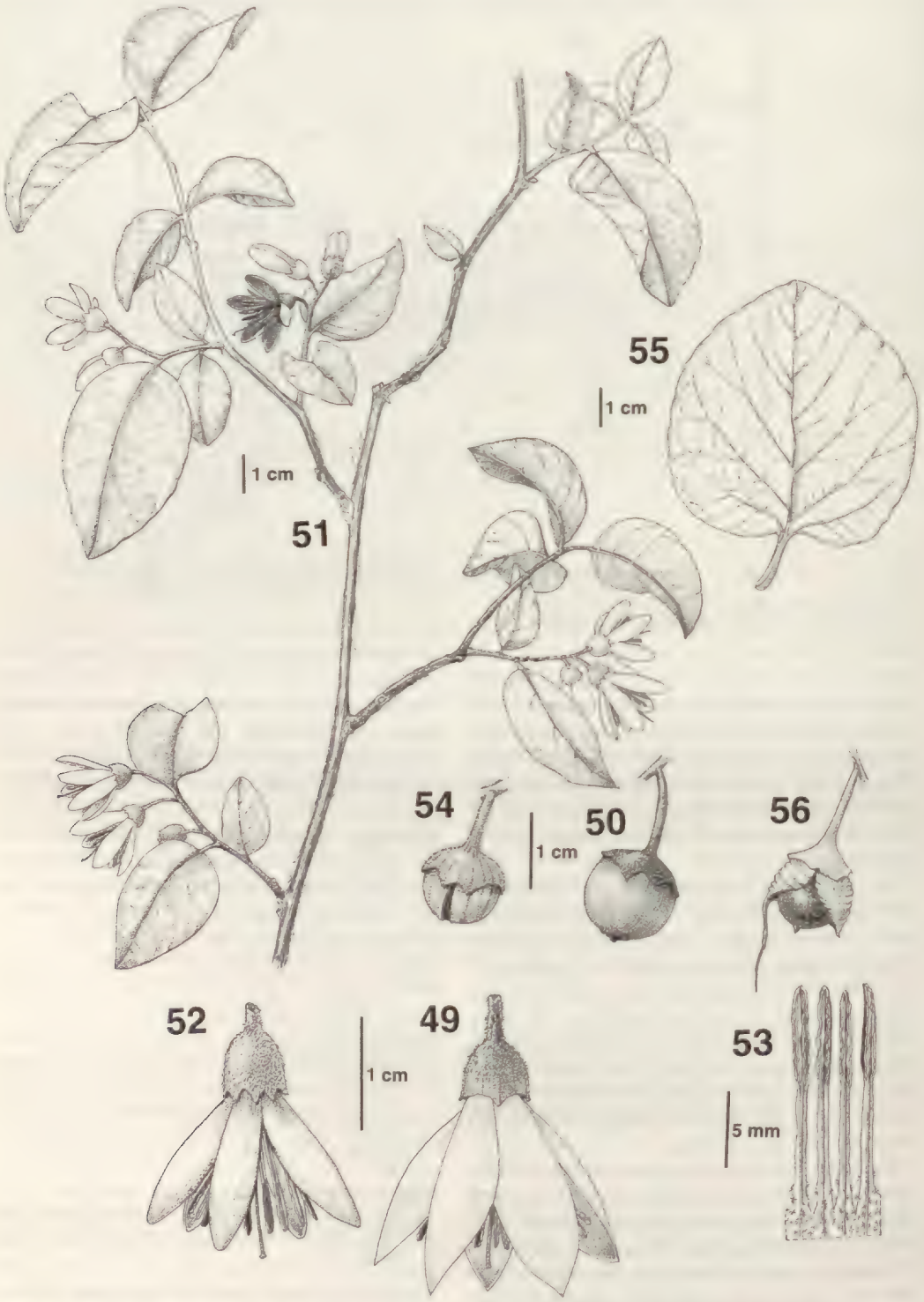
6. Styrax glabrescens Benth., Pl. hartw. 66. 1840. TYPE: Mexico. Oaxaca: [Chinantla region], planitie Llano Verde, *Hartweg 489* (holotype, K; isotype, LD not seen, photo in XAL not seen). Figures 48–50.

Styrax guatemalensis Donn. Sm., Bot. Gaz. 15: 27. 1890. TYPE: Guatemala. Alta Verapaz: Sasis, Apr. 1889, *H. Helmrich 1690* (holotype, US; isotype, GH).

Styrax glabrescens var. *pilosus* Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 72. 1907. *Styrax pilosus* (Perkins) Standl., Contr. U.S. Natl. Herb. 23: 1129. 1924. TYPE: Mexico. Oaxaca: Chinantla. May 1844, *H. Galeotti 2852* (lectotype, here designated, BR; isolectotypes, B destroyed, BR, F, LE not seen, NY, US, W).

Styrax vestitus Lundell, Wrightia 4: 121. 1969. TYPE: Mexico. Chiapas: Concordia, 16 June 1945, *E. Matuda 15922* (holotype, LL not seen, photocopy, LL; isotype, F).

Deciduous tree to 30 m. Young twigs densely whitish or yellowish stellate-pubescent or nearly glabrous, often with scattered orange-brown or dark brown stalked stellate hairs toward the base; outer layer of older twigs often exfoliating into long strips.



Figures 49–56. 49, 50. *Styrax glabrescens*. —49. Flower. *Calzada 4333* (F). —50. Fruit, *Cházaro 1511* (F). 51–54. *Styrax jaliscanus*. —51. Flowering branch. —52. Flower. —53. Four adjacent stamens. 51–53, *Pringle 11012* (F). —54. Fruit, *Breedlove 61642* (CAS). 55, 56. *Styrax platanifolius* subsp. *youngiae*, *Henrickson 11561* (TEX). —55. Leaf. —56. Fruit.

Petiole 6–16 mm long. Lowest leaf pair on each twig often subopposite or opposite. Lamina membranous, 3.5–14 × 1.5–10 cm on fertile branches [sometimes smaller and nearly bract-like; laminae of sterile branches nearly always larger (to 21 × 11 cm)], ovate or obovate, sometimes (especially the terminal leaf on sterile twigs) rhombic or suborbicular, secondary veins 6–8; lowest leaf pair often ovate-oblong; apex cuspidate to long-acuminate; base narrowly cuneate to rounded, rarely truncate or attenuate, symmetric or slightly oblique, the bases of lowest two leaves often oblique; adaxially glabrous except along the major veins; abaxially covered with white stellate hairs or more often glabrous or nearly so, often with scattered orange-brown or dark brown stalked stellate hairs especially prevalent on veins and the lowest pair of leaves on each shoot, the stellate portion often deciduous from the base, the veins glabrous or moderately pubescent; margin serrate or entire but always glandular, the teeth tipped by the glands. Inflorescences racemose or rarely paniculate, axillary or false-terminal, axillary racemes usually present, 1–5(–17)-flowered, shorter than the false-terminal raceme and occurring in the leaf axils immediately below it, sometimes more than one raceme occurring in the same leaf axil, false-terminal racemes 2–10.5 cm long, (1)2–12(–21)-flowered. Lower pedicels 3–10 mm long. Calyx 4–6 × 4–6 mm, campanulate or broadly cupuliform, grayish green-stellate-pubescent, often also with various amounts of yellow, orange-brown, or dark brown stellate hairs especially toward the base, more thinly pubescent within 1 mm from apex; calyx teeth 0–7, unevenly distributed, to 0.8 mm long, narrow-deltoid or linear, contiguous or separated by the truncate or slightly concave calyx margin, inner margin eglandular. Corolla white, 14–28 mm long, petals connate 0–2 mm beyond the calyx margin distally; corolla lobes 5(–10), imbricate in bud, 11–23 × 6–10 mm, overlapping, spreading, thin, elliptic or broadly elliptic, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube none; distinct portion of filament 6–9 mm long, of equal width throughout or narrowing distally, ventrally not auriculate, moderately densely white-stellate-pubescent on the face, becoming glabrous distally, the hairs with arms to 0.2 mm long; anthers 4–6 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary thinly or densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3–0.6 mm wide. Fruit 10–15(–17) × 9–15(–19)(wider when 2-seeded) mm, globose, indehiscent (rarely 3-valve-dehiscent), hard-walled; wall smooth (but stellate-pubescent). Seed coat glabrous.

Querétaro and northern Veracruz, Mexico, to southwestern Costa Rica; common on the eastern slopes of the Sierra Madre Oriental, becoming scattered southward to Nicaragua, but frequent on the Pacific slope of the cordillera in Costa Rica; 500–2600 m; evergreen cloud forest, temperate deciduous forest, montane rainforest of oak-pine, elfin forest, subdeciduous forest, bosque mesofilo de montaña; found frequently along waterways, also on steep slopes; in soil of high organic content or clay, often with rocks, in primary or secondary growth. Flowering: commonly December–May, rarely June, July; fruiting: throughout much of the year, but most commonly maturing April–September.

Common Names. Azucena (Guatemala, *Steyermark 49738*); jazmincillo (Veracruz, *López & Sosa 503*), palo blanco (Chiapas, *Calzada et al. 8791*; Querétaro, *Servín 15*), salamo (El Salvador), zapotillo (Veracruz, *Cházaro 1511* and *2691*); from Pacheco (1983): azahar del monte, cucharillo, flor de azahar, jazmín, zapotillo (Veracruz).

Uses. Firewood (Guatemala, *Steyermark 49738*).

Selected specimens examined. COSTA RICA. **Alajuela:** Reserva Forestal de San Ramón, valley of the Río Lorencito, *Burger et al. 12475* (CAS, DUKE, F). **Cartago:** near Río Patarrá, 2 km S of Muñeco, *Lent 1932* (AAU, CR, DUKE, F, MEXU, MO, NY). **Puntarenas:** around Río Canasta, 9.5 km NW of Agua Caliente, *Davidse et al. 28381* (CR, F, MO, TEX). **San José:** Pacific slope of Chirripó massif, *Davidse & Pohl 1656* (DUKE, MO, NY). EL SALVADOR. **Santa Ana:** Cerro Montecristo, 20 May 1976, *Reyna s.n.* (CR). GUATEMALA. **Alta Verapaz:** region of Cocolá, NE of Carchá, *Standley 70316* (F). **Baja Verapaz:** Niño Perdido, between km 151/152W, *Lundell & Contreras 21126* (CAS, LL, MEXU, MO, NY). **Huehuetenango:** Barillas, *Holdridge 2338* (F, US); Cerro Victoria, Sierra de los Cuchumatanes, *Steyermark 49738* (F). **Quezaltenango:** La Shuya, SW of San Martín Chile Verde, *Standley 67865* (F). **Quiché:** valley of Río de las Violetas, N of Nebaj, *Proctor 25210* (F, LL, MO). **San Marcos:** Volcán Tajumulco, 9 mi. S and W of Tajumulco, *Steyermark 36807* (F). **Suchitepéquez:** Volcán Santa Clara, *Steyermark 46750* (F). HONDURAS. **Comayagua:** near the summit of the range above El Achote, *Yuncker et al. 6175* (F, GH, MO, NY, U). **La Paz:** Montaña Verde on Cordillera Guajiquiro, *Molina & Molina 24404* (DS, F, NY). **Lempira:** 8.8 km al SE de Gracias, Parque Nacional de Celaque, *Darío 72* (DUKE). **Olancho:** along Río Olancho, 13.6 mi. SW of Gualaco, *Croat 64211* (DUKE). **Yoro:** Río Pijol Valley, 6 to 7 km S of Nueva Esperanza, *Liesner 26612* (DUKE). MEXICO. **Chiapas:** on the SE side of Cerro Tres Picos, *Breedlove 34377* (F, DS, DUKE, LL, MEXU, MICH, MO, NY, POM). **Guerrero:** 25 km al NE de Paraíso, *Núñez et al. 5243* (F, MEXU, MO). **Hidalgo:** river bluffs below Trinidad Iron Works, *Pringle 13104* (BH, CAS, F, GH, MICH, MO, US). **Oaxaca:** Dto. de Ixtlán, Mpio. de Comaltepec, *Martin 501* (CAS, MEXU, MO, NY, US). **Puebla:** Mpio. de Hueytamalco,

Colijuit, *Ventura 784* (DS, F, MICH, MO, US). **Querétaro:** 1.5 km al SE de La Yesca, *Rubio 1711* (MICH, MO, TEX). **San Luis Potosí:** Cerro de la Silleta, Cerca de Zilitla, *Paray 681* (MEXU, MICH). **Tamaulipas:** Sierra de Guatemala, *Sullivan 543* (DUKE, MO, NY, TEX). **Veracruz:** Rancho La Martinica, a 5 km al N del pueblo de Banderilla, *Calzada 4333* (F, MEXU); entre Coatepec y Coatepec Viejo, *Cházaro 1511* (F); hills near Jalapa, *Pringle 8129* (A, B, BH, BR, F, GH, MO, NY, POM, US, W). NICARAGUA. **Zelaya:** along trail from Cerro El Inocente toward Cerro Saslaya, *Stevens 6687* (MO).

Styrax glabrescens is one of the most common and widespread species of *Styrax* in the present revision, occurring from northeastern Mexico to southern Costa Rica. It appears to be most abundant in the cloud forests of central Veracruz, Mexico. It is the only deciduous member of the genus in the region with a tree habit; *S. platanifolius* and *S. jaliscanus* are shrubs that are multi-stemmed from the base. *Styrax glabratus* might at first be mistaken for *S. glabrescens* on the basis of its glabrous abaxial laminar surface, but it is evergreen and has a drupe instead of a dry fruit.

Perkins (1907) differentiated *Styrax glabrescens* var. *pilosus* from the typical variety on the basis of the dense pubescence on the lower laminar surface. Standley (1924) raised this taxon to the rank of species solely on this basis. Gonsoulin (1974) agreed with Perkins (1907), but in addition to the difference in leaf pubescence he distinguished variety *pilosus* from variety *glabrescens* by describing the calyx of variety *pilosus* as minutely grayish tomentulose, as opposed to rufous or yellowish pilose-stellate in variety *glabrescens*. Pacheco (1983) agreed with Standley, citing the leaf pubescence difference as well as the length of the inflorescence, the number of flowers, and the glaucous aspect of the leaves (on the lower laminar surface?) as justification for the delimitation of two species.

In my analysis of the problem I have found no basis for recognizing either two species or two varieties within *Styrax glabrescens*. The pubescent form of *S. glabrescens* has a distribution largely overlapping that of the glabrous form, occurring from Tamaulipas, Mexico, at the extreme northern edge of the species' range, south to Guatemala, whereas the glabrous form occurs throughout the range of the species. The pubescent form also exhibits no obvious elevation or habitat distinction, and seems to occur sporadically, often near collection localities of the glabrous form. Furthermore, several collections show an intermediate amount of pubescence between the types of *S. glabrescens* var. *pilosus* and variety *glabrescens*. Similar variation in pubescence amount without concomitant geographic distinction or ecological separation occurs in *S. grandifolius*, and that species was not treated as having varieties by Perkins (1907) or Gonsoulin (1974). *Styrax redivivus* in California also shows the same type of pubescence variation, but despite additional characters associated with the pubescence differences, varietal status on this basis was not considered warranted because the variation is distributed clinally (Fritsch, 1996b). To be taxonomically consistent, and considering the weak to nonexistent geographical and ecological bases for distinguishing either two species or two varieties within *S. glabrescens*, I have subsumed *S. glabrescens* var. *pilosus* (= *S. pilosus*) under *S. glabrescens*.

The protologue of *Styrax glabrescens* indicates a type collection date of April–July 1839. Gonsoulin (1974) incorrectly cited the type of *S. glabrescens* as "*Linden*, Jun 1838" at K.

A collection date of May 1844 is indicated on the lectotype of *S. glabrescens* var. *pilosus* (*Galeotti 2852*) [as well as on some of the isotypes of *S. cyathocalyx* (*Galeotti 1687*); see under *S. ramirezii*]. However, Galeotti had left Mexico by 1840 (McVaugh, 1978) and seems not to have returned. Early in the year of 1840 he was presumed to have visited northeast Oaxaca, where the *2852* collection was made. If a transcription error occurred on the *2852* labels, then it is likely that the collection was made in 1840. I have found no additional information that explains the discrepancy. Some type specimens of *S. glabrescens* var. *pilosus* are designated "*3852*" and are presumably the result of a transcription error.

In the protologue of *Styrax glabrescens* var. *pilosus*, Perkins (1907) specifically listed two specimens of the type collection *Galeotti 2852:* B and BR; thus, these are technically syntypes and a lectotypification of this name is in order. Because the B specimen has been destroyed, I have chosen the two BR sheets (here interpreted as constituting a single specimen) as the lectotype.

The collection date of the type of *Styrax vestitus* is 16 June 1945 according to the label information, but 14 June 1945 according to the protologue. Also regarding *S. vestitus*, the collection number of the type is *5922* in the protologue and on the photocopy of the holotype, but *15922* on the F isotype.

7. **Styrax incarnatus** P. W. Fritsch, sp. nov. TYPE: Guatemala. Baja Verapaz: Niño Perdido, La Cumbre de San José Espinero, 20 May 1977, *C. L. Lundell & E. Contreras 20933* (holotype, CAS; isotypes, LL, MEXU, MO, NY). Figures 28–30, 47.

Arbor sempervirens; *lamina* crassi-chartacea, 12–17 × 5.5–9.5 cm longa, ovata vel late elliptica, subtus pilis densis cinerascentibus-viridibus-stellatis et dispersis ferrugineis-stellatis instructa, venis secondariis et tertiariis occultis a tomento; *pedicelli* inferiores 3–9 mm longi; *calyx* 3–3.5 × 2.5–4.5 mm, stellata-pubescens; *corolla* (10–)15–24 mm longa, lobis in aestivatione valvatis, sub anthesi apertis; *filamenta* staminum partibus distinctis ad margines ventrales pilis stellatis aequiliter dispersis instructa, aliter fere glabra ventraliter praeter ad apices, brachis pilorum plus minusve radiatis ex axibus centralibus; *connectivum* antherae loculos non-contractos non vel leviter superans.

Evergreen tree to 21 m. Young twigs dark orange-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 10–17 mm long. Lamina thick-chartaceous, 12–17 × 5.5–9.5 cm, ovate or broadly elliptic, secondary veins 12–15; apex acute to abruptly acuminate; base subrounded to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute greenish white stellate hairs, larger greenish white stellate hairs with arms to about 0.3 mm long, and somewhat larger orange-brown stellate hairs, the latter particularly prevalent near and on the major veins, the minute and larger whitish hairs occurring on the secondary and tertiary veins thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 5–9 cm long, 3–7-flowered. Lower pedicels 3–9 mm long. Calyx 3–3.5 × 2.5–4.5 mm, conical with rounded base, greenish white-stellate-pubescent with somewhat larger scattered orange-brown stellate hairs toward the base; calyx teeth 5, to 0.5 mm long, deltoid, the calyx margin concave between the teeth, inner margin often glandular. Corolla pink or purplish pink, (10–)15–24 mm long, petals connate (2–)4–7 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, (6–)9–16 × 2–4 mm, non-overlapping, nearly erect or moderately spreading, linear, thickened, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube (1–)3.5 mm long; distinct portion of filament (1–)2 mm long, of equal width throughout, ventrally not auriculate, sparsely pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.3 mm long; anthers (4–)5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style with a few hairs at base only; stigma 0.5 mm wide. Largest drupe observed (only immature fruits available for study) 9 × 6 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat observed immature.

Rare, occurring in the departments of Baja Verapaz and Alta Verapaz, Guatemala, and the department of Comayagua, Honduras; 1900 m; "in high forest," cloud forest of mixed hardwood species. Flowering: May, August, November; fruiting: immature fruit in November.

Additional specimens examined. GUATEMALA. **Baja Verapaz:** Unión Barrios, NW of km 159 of the road, *Lundell & Contreras 19450* (LL, MO); Unión Barrios, W of km 159 of the road, *Lundell & Contreras 19618* (CAS, LL). HONDURAS. **Comayagua:** trail to San Juanillo of the Cordillera de Montecillos, *Thomas 26* (DUKE).

Styrax incarnatus is a rare endemic to Guatemala and Honduras. Of the *Styrax* species that grow in Guatemala and Honduras it resembles most closely *S. warscewiczii*, from which it is easily distinguished by its much larger leaves, stellate-pubescent calyx, and usually larger flowers. The species also resembles *S. austromexicanus*, which differs mainly in its narrowly elliptic leaves, shorter pedicels, and smaller calyces.

The sole Honduran collection (*Thomas 26*) has shorter corollas than the Guatemalan collections, but matches them otherwise. More collections, especially those in fruit, would help clarify the degree of character variation, natural history, and evolution of this species.

8. Styrax jaliscanus S. Watson, Proc. Amer. Acad. Arts 26: 144. 1891. *Styrax officinalis* L. var. *jaliscanus* (S. Watson) Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 82. 1907. TYPE: Mexico. Jalisco: Sierra de San Esteban near Guadalajara, 10 Nov. 1889, *C. G. Pringle 2978* (lectotype, here designated, GH; isolectotype, A). Figures 40, 51–54.

Deciduous shrub multi-stemmed from the base, to 2 m. Young twigs densely white-stellate-pubescent, often toward the base with scattered orange-brown or dark brown stalked stellate hairs; outer layer of older twigs often exfoliating into long strips. Petiole 4–5 mm long. Lamina chartaceous, 5–13 × 3.2–8 cm, orbicular, ovate-orbicular, broadly elliptic, or obovate, often slightly conduplicate, as evidenced by the longitudinally folded laminae on herbarium specimens, secondary veins 7–10; apex acute, cuspidate, or abruptly acuminate; base subcuneate or rounded, rarely subcordate, sometimes slightly attenuate, if subcordate then not at all attenuate, symmetric or slightly oblique; adaxially stellate-pubescent; abaxially thickly covered with white stellate hairs, often with scattered orange-brown or dark brown stalked stellate hairs especially prevalent on veins and the lowest pair of leaves

on each shoot, the stellate portion often deciduous from the base, sometimes old leaves more sparsely tomentose, the veins tomentose or nearly glabrous, secondary and tertiary veins prominent; margin serrulate or entire, glandular or eglandular, the teeth tipped by the glands. Inflorescences axillary or false-terminal, racemose, sometimes contracted and thus appearing umbellate, axillary racemes usually present, 1-flowered and occurring in the leaf axils immediately below the false-terminal raceme, false-terminal racemes 2.2–5.5 cm long, (1–)3–9-flowered. Lower pedicels 2–11 mm long. Calyx 3–7 × 4–6 mm, campanulate, grayish green-stellate-pubescent; calyx teeth 5–7, unevenly distributed, to 2 mm long, narrowly deltoid or deltoid, usually contiguous, inner margin eglandular. Corolla white, 9–16 mm long, petals connate up to the calyx margin; corolla lobes 5(–10), imbricate in bud, 6–14 × 4–5 mm, overlapping, spreading, thin, broadly elliptic or obovate, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0.5–1.5 mm long; distinct portion of filament 4–6 mm long, of equal width throughout or sometimes narrowing distally, ventrally not auriculate, sparsely white-stellate-pubescent on the face, becoming glabrous distally, the hairs with arms to 0.15 mm long; anthers 4–4.5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely short-stellate-pubescent; style glabrous or pubescent at base only; stigma 0.3–0.7 mm wide. Capsule 8–11 × 7–11 mm, globose, 3-valve-dehiscent, the wall hard, stellate-canescent, coarsely and weakly longitudinally striate, not transversely wrinkled post-dehiscence. Seed coat glabrous.

Rare, occurring in southern Nayarit and adjacent portions of Jalisco, Mexico; 832–1700 m; *Quercus* or *Quercus-Pinus* forests; found in rocky places. Flowering: April–July; fruiting: September–December.

Additional specimens examined. MEXICO. **Jalisco:** S rim of the Barranca del Río Santiago, *Breedlove 61642* (CAS, MICH, NY); between km 17 and 18 on Hwy. Guadalajara–San Cristóbal de la Barranca, *Calzada et al. 17816* (MICH, RSA); Mpio. de Zapopan, Cerro del Diente, *Cházaro & Cházaro 6993* (TEX), *Guerrero et al. 322* (WIS); La Piedrera, *Nieves 50* (MEXU); Mpio. de Ahualulco, al NW de Chapulimita, 17 Sep. 1987, *Pérez s.n.* (IBUG); rocky hills near Guadalajara, *Pringle 3486* (GH); Sierra de San Esteban, *Pringle 4416* (F, MEXU, MICH, MO, NY, US, W), *Pringle 11012* (BH, F, GH, MICH, MO, NY, US); Mpio. de Zapopan, La Mesita de Sta. Lucía, *Ramírez 259* (IBUG); Guachinango, 20 Nov. 1982, *Robles s.n.* (IBUG); San Cristóbal de la Barranca, *Salazar 5* (IBUG); carretera a San Cristóbal de la Barranca, km 18, *Velázquez 13* (IBUG); Cerro del Tepopote, 20 km al W de Guadalajara, *Villarreal 4585* (IBUG, MICH). **Nayarit:** 8 km SE of San Leonel on Hwy. 15, *Breedlove & Almeda 45097* (CAS); km 192 on Hwy. 15 going NW from Tequila to Tepic, *Calzada et al. 17822* (MICH, RSA); 15 km NE of Santa Cruz de Guaybel, *Cházaro et al. 5485* (WIS); Ocotillo, *Gregg 955* (MO); between Ocotillo and Jazmines, ca. 25 mi. SE of Tepic, *McVaugh 12061* (MICH); 5 mi. SE of San Leonel, *McVaugh 13369* (MICH).

Styrax jaliscanus is the only deciduous *Styrax* species in western Mexico, so it is easily distinguishable from other sympatric members of the genus. This species was first collected near Ocotillo, Nayarit [28 May 1849, *Gregg s.n.*, date from McVaugh (1972)], but was left undescribed until Watson examined Pringle's 1889 collections. Perkins (1907) considered this species a variety of *S. officinalis* L., conferring upon the latter a highly disjunct distribution between southwestern Mexico, California, and the eastern Mediterranean region. *Styrax jaliscanus* does superficially resemble *S. officinalis* in its often orbicular and entire-margined leaves that are densely tomentose abaxially, and often contracted racemes. Upon closer inspection, however, the differences between these two species become apparent, including usually serrate versus always entire leaf margins, and prominent versus weak secondary and tertiary veins abaxially in *S. jaliscanus* and *S. officinalis*, respectively. The Californian representatives of *S. officinalis* have recently been treated as a species (*S. redivivus*) separate from *S. officinalis* in the Mediterranean region. Molecular phylogenetic analysis has confirmed that the relationship of *S. jaliscanus* to the lineage comprising deciduous *Styrax* taxa with entire leaf margins (*S. officinalis*, *S. platanifolius*, and *S. redivivus*) is distant (Fritsch, 1995, 1996a). According to the molecular data, *S. jaliscanus* is positioned in the same clade as the other deciduous, serrate-leaved species, i.e., the North American species *S. americanus*, *S. glabrescens*, and *S. grandifolius*, and many species of eastern Asia (Fritsch, 1995). Thus, I agree with Gonsoulin (1974) in maintaining species status for *S. jaliscanus*.

Gonsoulin (1974) reported *S. jaliscanus* to be a wide-ranging but sporadic species, occurring from extreme northern Baja California to Guerrero, Mexico. However, Gonsoulin made several errors concerning the range of this species: (1) he mistook two collections of *S. gentryi* (*Gentry 4420*, from Baja California Sur, and *Gentry 6244*, from Sinaloa) for *S. jaliscanus*; (2) he supposed that the Sierra de la Laguna is at the northern end of Baja California rather than the Cape Region of Baja California Sur; and (3) the Guerrero collection is cited in the revision as *Hinton 4583*; according to Hinton's collection list (Hinton & Rzedowski, 1972), this

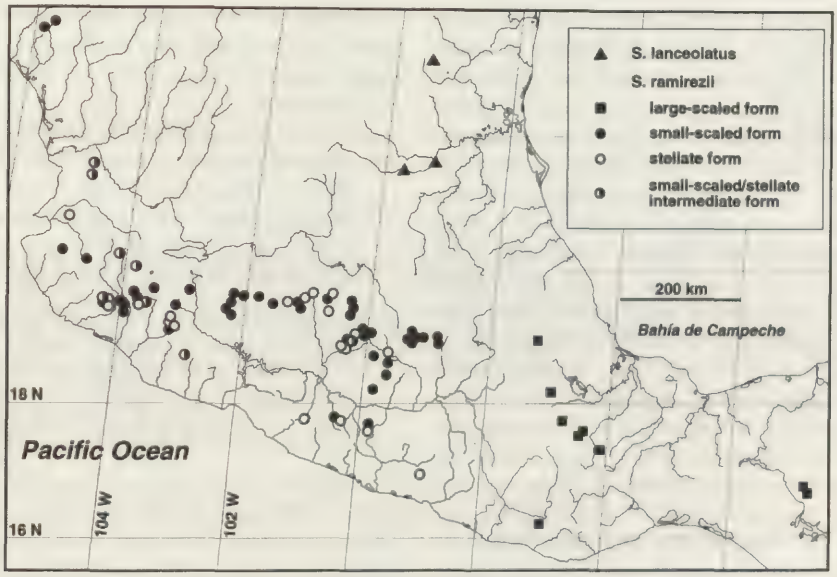


Figure 57. Distribution of *Styrax lanceolatus* and the forms of *S. ramirezii*.

number is actually *Apodanthera pringlei* S. Watson of the Cucurbitaceae, which could not possibly be mistaken for *Styrax*. There is no apparent explanation for Gonsoulin's erroneous citation of the Hinton collection—I do not know of any *S. jaliscanus* collections made by Hinton or anyone else from Guerrero.

Styrax jaliscanus, as circumscribed here, is a rare endemic to western Jalisco and Nayarit, Mexico. It was probably at one time more common in the hills surrounding Guadalajara, but habitat degradation resulting from overgrazing and fires has undoubtedly led to its decline there (pers. obs.). The risk of this species becoming extinct appears to be high. A detailed study entailing the documentation of all known populations, exploration within the range for yet undocumented populations, observation of life history parameters, examination of genetic variation patterns, and identification of threats to survival would help to identify the causes and possible mitigating measures that could be taken in order to protect this species. Toward this end, two populations of *S. jaliscanus* have been sampled for isozyme variation (Fritsch, 1996a).

I have selected the lectotype from two syntypes (*Pringle 2978* and *Pringle 3486*) cited in the protologue. I considered it best to designate *Pringle 2978* (GH) as the lectotype because (1) Gonsoulin (1974) cited *Pringle 2978* as the holotype and (2) Watson's original herbaria were US and GH (i.e., not A; Stafleu & Cowan, 1988).

The collection date of the type of *S. jaliscanus* is given as "1889" on labels but "1890" in the protologue.

9. Styrax lanceolatus P. W. Fritsch, nom. et stat. nov. Based on: *Styrax argenteus* var. *parvifolius* E. Carranza, Acta Bot. Mex. 23: 35. 1993. TYPE: Mexico. Querétaro: Mpio. de Arroyo Seco, ± 2 km al W de Agua Fría de los Fresnos, 23 Apr. 1992, *E. Carranza 4033* (holotype, IEB not seen; isotypes, CAS, ENCB not seen, MEXU not seen, MICH, XAL not seen). Figures 31, 57.

Evergreen tree to 6 m. Young twigs grayish green- or brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 7–12 mm long. Lamina chartaceous, 7.7–9.7 × 3.0–3.9 cm, lanceolate; apex narrowly acute to acuminate, secondary veins 8–9; base broadly cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with greenish white stellate hairs and scattered light orange-brown hairs on at least some leaves, the latter particularly prevalent near the veins, the whitish hairs covering on the secondary and tertiary veins, thus obscuring the vein surface; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 1.7–5.0 cm long, 1–8-flowered. Lower pedicels 3–5 mm long. Calyx 3.5–4.5 × 4.5–6.0 mm, broadly cupuliform, grayish green-stellate-pubescent, with scattered orange-brown stellate hairs,

especially toward the base; calyx teeth 5, sometimes absent, to 0.3 mm long, deltoid, the calyx margin slightly concave between the teeth, or if teeth absent then margin truncate, inner margin often glandular. Corolla white (Carranza, 1993), 11–15(–17 according to Carranza, 1993) mm long, petals connate to just beyond the calyx margin distally; corolla lobes 5, valvate in bud, 8–11 × 1.5–2.5 mm, non-overlapping, slightly spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 4 mm long; distinct portion of filament 0.7–2.0 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, sparsely pubescent on the face proximally, increasing in pubescence distally, the hairs with arms to 0.5 mm long; anthers 3.5–4 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-tomentose; style and stigma not observed. Drupe 9–10(–11, according to Carranza, 1993) × 7–8(–9, according to Carranza, 1993) mm, ovoid-cylindric; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Rare in southern Tamaulipas and northern Querétaro, Mexico; 800–1500 m; *Quercus-Podocarpus* forests, wet forests; in Querétaro, found on hillsides and disturbed sites (Carranza, 1993). Flowering: October–January; fruiting: January–April (Carranza, 1993).

Uses. Occasionally made into posts in the construction of dwellings (Carranza, 1993).

Additional specimens examined. MEXICO. **Querétaro:** 2 km al W de Agua Fría de Los Fresnos, *Carranza 4465* (CAS). **Tamaulipas:** Rancho El Cielo, *Fairey T26M-79p-101490* (MICH, RSA); Gómez Farias region, *Johnston 7408* (TEX); Casa Piedra, ca. 2 km SW of Rancho del Cielo, *Johnston 12845* (TEX).

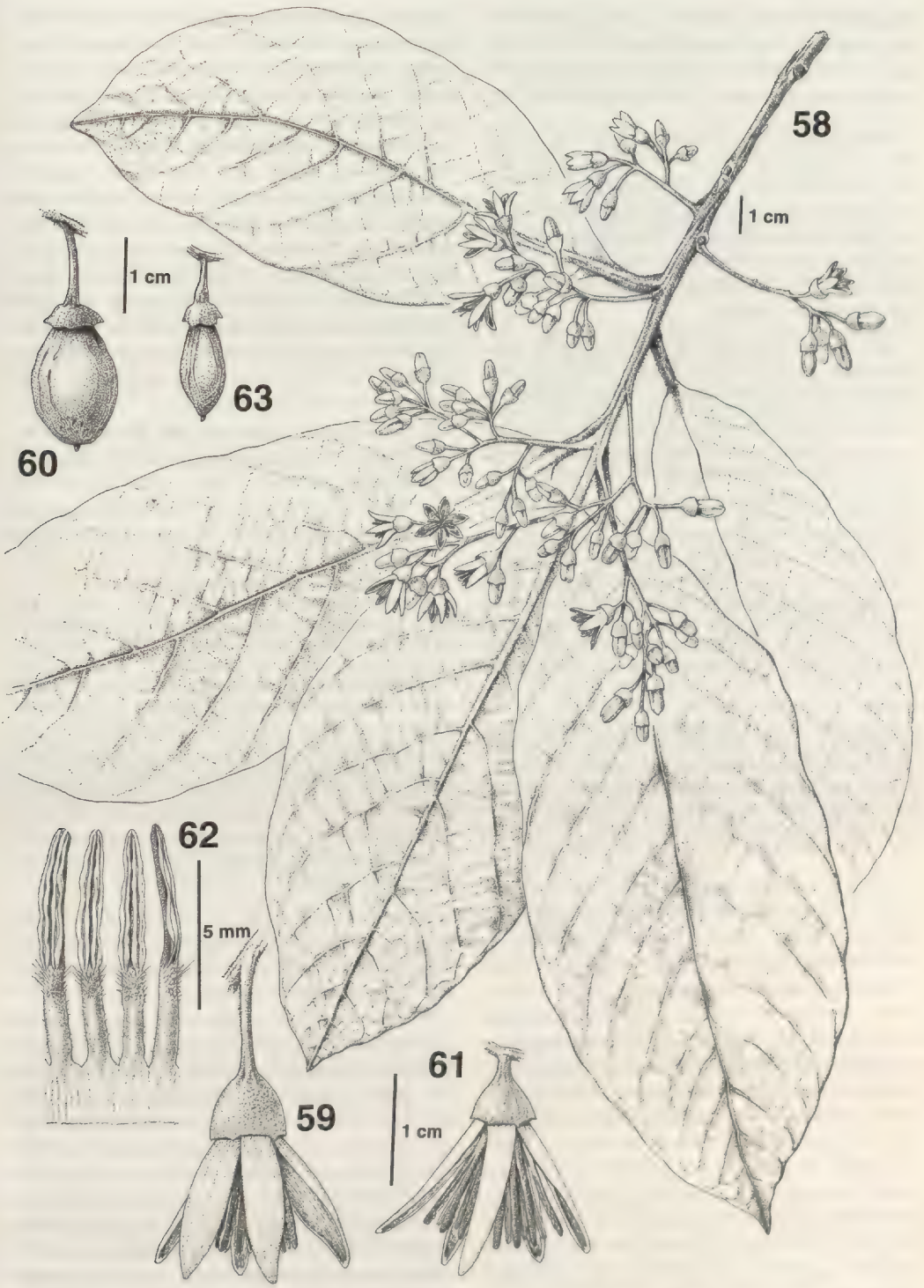
Styrax lanceolatus is a recently described rare endemic to southern Tamaulipas and western Querétaro, Mexico. It differs from sympatric species by its evergreen habit and stellate-pubescent calyx.

Carranza (1993) considered this species to be a variety of *Styrax argenteus* (var. *parvifolius*). However, in contrast to *S. argenteus* as circumscribed here, *S. lanceolatus* has non-tapered anther sacs, non-prolonged anther connectives, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. *Styrax warscewiczii* has many features in common with *S. lanceolatus,* but usually does not have the distinctive lanceolate leaves and always has a radiate-lepidote rather than a stellate-pubescent calyx. In addition, the ranges of *S. lanceolatus* and *S. warscewiczii* are nearly or completely non-overlapping (depending on the status of *Purpus 5317*; see discussion under *S. warscewiczii*).

10. Styrax magnus Lundell, Bull. Torrey Bot. Club 66: 600. 1939. TYPE: Mexico. Chiapas: Volcán Tacaná north, 2 Apr. 1939, *E. Matuda 2982* (holotype, MICH; isotypes, A, B, F, GH, MICH, MO, NY, US). Figures 32, 58–60.

Styrax vulcanicola Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 264. 1940. TYPE: Guatemala. Dept. San Marcos: between town of Tajumulco and Tecutla (9 mi. S and W of Tajumulco), northwestern slopes of Volcán Tajumulco, 27 Feb. 1940, *J. A. Steyermark 36801* (holotype, F (2 sheets)).

Evergreen tree to 26 m. Young twigs orange-brown-stellate-pubescent, sometimes mixed with smaller greenish white hairs; outer layer of older twigs not exfoliating. Petiole 17–30 mm long. Lamina chartaceous, 15.5–22.5 × 6.8–12 cm, usually obovate, sometimes broadly elliptic, secondary veins 10–20; apex abruptly short-acuminate to rounded; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute white stellate hairs and also variable amounts of larger white, rarely also orange-brown stellate and somewhat stiff hairs, the latter usually occurring on the veins, the minute hairs absent from the primary through tertiary veins thus the vein surface easily visible; margin entire. Inflorescences axillary or false-terminal, paniculate or rarely racemose, the racemes or panicle branches 1.5–4 cm long, 2–10-flowered. Lower pedicels 6–15 mm long. Calyx 3.5–5 × 4.5–6 mm, cupuliform or broadly cupuliform, grayish green-stellate-pubescent, occasionally with scattered larger orange-brown stellate hairs toward the base; calyx teeth 5, to 0.6 mm long, deltoid, the calyx margin truncate or slightly concave between the teeth, inner margin often glandular. Corolla white, (7–)11–12 mm long, petals connate 0–2 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, (7–)8–10 × (2–)3 mm, non-overlapping, spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 2 mm long; distinct portion of filament 1.0–1.2 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.5 mm long; anthers 5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely



Figures 58–63. 58–60. *Styrax magnus*. —58. Flowering branch. —59. Flower. 58, 59, *Breedlove 68742* (CAS). —60. Fruit, *Breedlove 46223* (CAS). 61–63. *Styrax radians*. —61. Flower, *McVaugh & Koelz 541* (MICH). —62. Four adjacent stamens. —63. Fruit. 62, 63, *Tenorio 15605* (MO).

stellate-hirsute; style glabrous or pubescent at base only; stigma 0.5 mm wide. Drupe 15–20 × 9–12 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Uncommon in the central and southern mountains in Chiapas, Mexico, extending into south-central Guatemala along the Pacific slope; 1700–2700 m; montane rainforests and dry forests, evergreen and mixed forests, *Magnolia-Podocarpus* and *Quercus-Drimys* forests; found on dry ridges, on volcanic slopes, in sandy soil. Flowering: May, August; fruiting: September–January.

Additional specimens examined. GUATEMALA. **Quezaltenango:** above Mujuliá, *Standley 85559* (F). **San Marcos:** Barranco Eminencia, above San Rafael Pie de la Cuesta, *Standley 68618* (F); Río Vega, near San Rafael, *Steyermark 36234* (F). MEXICO. **Chiapas:** near summit of Huitepec, *Alexander 1214* (MICH, NY); 45–50 km NE of Huixtla, *Breedlove & Thorne 31045* (DS, MEXU, MO); SW side of Cerro Mozotal, *Breedlove & Thorne 31106* (DS, MEXU, MO); Selva Negra, 10 km above Rayón Mezcalapa, *Breedlove & Smith 32394* (B, DS, DUKE, F, LL, MEXU, MICH, MO, NY, RSA); near the summit of Muk'ta vits (Cerro Huitepec), *Breedlove 39600* (DS, MO, RSA); near the summit of Muk'ta vits (Cerro Huitepec), *Breedlove 41446* (DS, MO, TEX, US); E slope Cerro Mozotal along road from Huixtla to El Porvenir, *Breedlove & Strother 46223* (CAS, LL, MEXU); near Colonia Ach'lum, *Breedlove 49750* (CAS, DUKE, TEX); near Paraje Banabil, *Breedlove & Almeda 57053* (CAS, MEXU, MO); E slope of Cerro Muk'ta vits, *Breedlove 68742* (CAS); 25 km al NE de San Cristóbal de las Casas, *Cabrera et al. 3805* (MO); Pueblo Nuevo a Simojovel, *Miranda 9170* (US); La Yerbabuena, al NW de Pueblo Nuevo Solistahuacán, *Palacios 161* (CAS); Cerro Huitepec al W de San Cristóbal, *Ton 7963* (CAS, F, MO); Santa Cruz en San Filipe, *Ton & Concepción 9734* (CAS, GH, MICH, MO, NY, TEX).

Styrax magnus is endemic to the broad summit of the Chiapas Plateau's wet eastern escarpment and the volcanic slopes of the Sierra Madre in southern Chiapas and southwestern Guatemala, although the species seems to be relatively common within its narrowly restricted geographic range. The large, usually obovate leaves readily distinguish it from other sympatric species of *Styrax*. *Styrax argenteus* occurs at lower elevations and often has leaves nearly as large as those of *S. magnus*, but they are not obovate. *Styrax incarnatus* has leaves of similar size and could conceivably be found within the range of *S. magnus*. However, its leaves are ovate or broadly elliptic and thick-chartaceous, with the secondary and tertiary veins completely covered by pubescence abaxially; the leaves of *S. magnus* are chartaceous, with the abaxial surfaces of the veins visible through the pubescence.

Gonsoulin (1974) subsumed *Styrax magnus* under his *S. argenteus* var. *hintonii*. I have maintained *S. magnus* as a species and assigned most of the remaining specimens annotated by Gonsoulin as *S. argenteus* var. *hintonii* to the stellate form of *S. ramirezii*. There are two consistently reliable characters that distinguish *S. magnus* from *S. ramirezii*: the consistently larger mature drupe of *S. magnus*, and the rather subtle leaf-shape difference between the two species. Two other features of *S. magnus* (branched, many-flowered inflorescences, more widely spreading corolla lobes) also delimit this species from *S. ramirezii*, but are not always present. The individuals of *S. ramirezii* that have been collected within the range of *S. magnus* are all the large-scaled form of the species and are easily distinguished from *S. magnus* by the radiate-lepidote calyx.

11. Styrax nicaraguensis P. W. Fritsch, sp. nov. TYPE: Nicaragua. Matagalpa: Cordillera de Darién, 28–31 mi. NE of Sebaco, 21 July 1962, *G. L. Webster et al. 12496* (holotype, MO; isotypes, DUKE, F, GH, LL, U). Figures 17–21, 47.

Arbor sempervirens; *lamina* 2.1–3.0plo longior quam latior, subtus pilis densis cinerascentibus-viridibus-stellatis et dispersis ferrugineis-stellatis instructa; *calyx* pilis densis cinerascentibus-viridibus-stellatis et saepe dispersis ferrugineis-stellatis instructus; *corolla* lobis in aestivatione valvatis, 2.5–4.0 mm latis, sub anthesi apertis, recurvis vel reflexis, linearibus-deltoideis; *filamenta* staminum partibus distinctis ad margines ventrales auriculatis, auriculis pilis albis-stellatis dense instructis, brachis pilorum usque ad 1.0 mm longis, illis pilorum apicem versus pro parte maxima ordinatis apicem floralibus versus; *antherae* 5.8–7.8 mm longae; *connectivum* antherae loculos contractos manifeste superans; *drupae* longiores 17–28 mm longae, ovoideae vel obovoideae.

Evergreen tree to 25 m. Young twigs orange-, yellow-, or gray-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 11–16 mm long. Lamina chartaceous, 8.5–14.5 × 3.4–5 cm, 2.1–3.0 times as long as wide, elliptic or ovate-oblong, secondary veins 8–11; apex narrowly acute to acuminate; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially densely covered with short-armed, grayish green stellate hairs and scattered larger orange-brown stellate hairs, the latter particularly prevalent near and on the veins, the secondary and tertiary veins glabrous or pubescent; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, racemes or panicle branches 2.3–7 cm long, 2–10-flowered. Lower pedicels 5–9 mm long. Calyx 3.5–5 × 4–6 mm, cupuliform, grayish green-stellate-pubescent, often with larger orange-brown stellate hairs especially toward the base; calyx teeth 5, to 0.3 mm long,

deltoid, calyx margin truncate between the teeth, inner margin often glandular. Corolla white, 13–15 mm long, petals not or only slightly connate beyond the calyx margin distally; corolla lobes 5, valvate in bud, 9–11 × 2.5–4 mm, non-overlapping, recurved or reflexed, thin, linear-deltoid, vesture on the outer distal third of the lobes consisting predominantly of radiate scales, best seen in the mature bud stage. Free portion of stamen tube 1.5 mm long; distinct portion of filament 2 mm long, of equal width throughout, ventrally with auricles bearing a dense mass of stiff white stellate hairs with arms to 1.0 mm long, also pubescent below the auricles and at the sinus between adjacent filaments, the hairs nearest the distal end of the filament with arms predominantly pointing upward; anthers 5.8–7.8 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3 mm wide. Drupe (15–)17–28 × (10–)11–14(–15 if 2-seeded) mm, ovoid or obovoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Northwestern Nicaragua and northwestern Costa Rica; 1100–1550 m.

Styrax nicaraguensis is a rare endemic with a disjunct distribution in the cloud forests of northwestern Nicaragua and northwestern Costa Rica. This disjunction reflects a paucity of high mountainous regions with cloud forest habitat between the two areas where it is known to exist. Enough time has apparently elapsed during separation for the disjuncts to have differentiated morphologically; hence, two subspecies have been designated here.

This species is probably the closest relative of *S. argenteus,* from which it can be distinguished by the presence of orange-brown hairs on the calyx and lower laminar surface, and the shorter stiff, long-armed, upward-pointing stellate hairs on the stamen filaments ventrally. Although *S. argenteus* does reach up to 1500 m elevation in many parts of its range, it does not occur in cloud forest habitat where *S. nicaraguensis* occurs.

Gonsoulin (1974) identified the only collection of this species seen by him at the time of his revision (*Williams 23955*) as *Styrax argenteus* var. *argenteus* (the annotation label on one of the duplicates states "close to var. *ramirezii*"). Because these specimens are either sterile or possess inflorescences with only pedicels and calyces, it is understandable that Gonsoulin overlooked the subtle vegetative differences between this species and the others in Central America. However, the collection Gonsoulin saw does present unusual features with respect to the rest of the material available to him, and it is surprising that no mention was made of this in his revision.

KEY TO THE SUBSPECIES OF *STYRAX NICARAGUENSIS*

1a. Fruiting calyx ± rotate; drupe ovoid, deeply rugose on herbarium specimens ..... 11a. *S. nicaraguensis* subsp. *nicaraguensis*

1b. Fruiting calyx cupuliform; drupe obovoid, shallowly rugose on herbarium specimens ..... 11b. *S. nicaraguensis* subsp. *ellipsoidalis*

11a. Styrax nicaraguensis subsp. **nicaraguensis**. Figures 17–20, 47.

Fruiting calyx ± rotate; drupe 17–21 × 13–14 (–15 if 2-seeded) mm, ovoid, deeply rugose on herbarium specimens.

Rare in northwestern Nicaragua; 1300–1550 m; cloud forests. Flowering: June–July; fruiting: June.

Additional specimens examined. NICARAGUA. **Estelí:** Laguna de Miraflores, *Atwood A316* (MEXU, MO, NY). **Jinotega:** Laguna de Miraflores, 8 June 1975, *Atwood s.n.* (MO); km 146 carretera Matagalpa–Jinotega, *Moreno 16366* (MO); along Hwy. 3, ca. 1 km NW of La Fundadora entrance, *Stevens & Henrich 20401* (MO). **Matagalpa:** Sta. María de Ostuma, *Williams et al. 23955* (F, NY, US, W).

11b. Styrax nicaraguensis subsp. **ellipsoidalis** P. W. Fritsch, subsp. nov. TYPE: Costa Rica. Puntarenas: Cordillera de Tilarán, Monteverde Comunidad, 6 June 1977, *V. J. Dryer 1420* (holotype, F; isotypes, CR, MO). Figures 21, 47.

Calyx fructifer cupuliformis; *drupa* (15–)19–28 × (10–)11–13 mm, obovoidea, rugosa tenuiter in sicco.

Fruiting calyx cupuliform; drupe (15–)19–28 × (10–)11–13 mm, obovoid, shallowly rugose on herbarium specimens.

Northwestern Costa Rica in the Cordillera de Guanacaste and the Cordillera Tilarán on the Pacific slope; 1100–1500 m; forest edges. Flowering: July, November; fruiting: April–June.

Additional specimens examined. COSTA RICA. **Guanacaste:** Cerro Cacao, *Chávez 540* (CR, INB); Parque Nacional Guanacaste Estación Mengo, Cerro Cacao *II INBio 164* (CR, MO). **Puntarenas:** Río Guacimal, *Bello 932* (CR, INB); Monteverde, *Dryer 1420* (CR, F), *Dryer 1575* (CR, MO), *Fuentes 192* (INB, MO), *Haber 230* (AAU, CR, MO); in Mata's pasture, Monteverde, *Hartshorn 1894* (CR, F, MO).

The *II INBio 164* collection has smaller leaves and fruit (15 × 10 mm) than other collections, but its other features leave no doubt as to its identity.

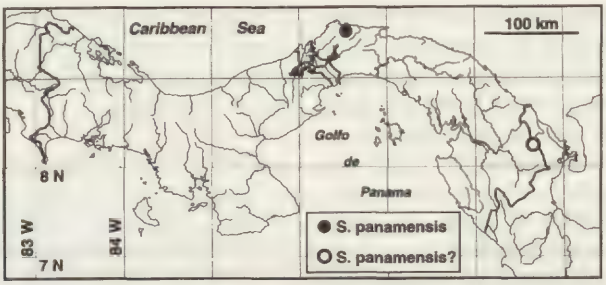


Figure 64. Distribution of *Styrax panamensis*; see text for explanation of dubious record.

12. Styrax panamensis Standl., Contr. U.S. Natl. Herb. 18: 121. 1916. TYPE: Panama. Colón: Loma de la Gloria, near Fató (Nombre de Dios), July and Aug. 1911, *H. Pittier 4242* (holotype, US-679343; isotypes, GH, NY, US). Figures 11, 64.

Evergreen tree to 10 m. Young twigs golden brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 6–16 mm long. Lamina chartaceous, 11.5–12 × 8–8.2 cm, 1.5 times as long as wide, broadly obovate, secondary veins 6–8; base cuneate, symmetric or slightly oblique; apex acuminate or emarginate through abortive tip development; adaxially glabrous except along the major veins; abaxially covered with minute white stellate hairs and scattered larger, grayish white, somewhat stiff stellate hairs, the latter occurring most frequently on the veins, the minute hairs absent from the primary through tertiary veins thus the vein surface easily visible; margin entire. Specimens in bud only. Inflorescences racemose, axillary or false-terminal, 3–4.5 cm long. Lower pedicels 5 mm long. Calyx 6 × 5 mm, narrowly cupuliform, uniformly golden brown-stellate-pubescent; calyx teeth 5, minute, deltoid, the calyx margin truncate or slightly concave between the teeth, inner margin apparently eglandular. Corolla in bud 11 mm long; corolla lobes 5, valvate in bud, 7–8 × 2 mm, linear-deltoid, vesture of the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0.8 mm long; distinct portion of filament 0.8 mm long, slightly flexuous, of equal width throughout, ventrally not auriculate, densely covered across the face with tawny, undulating to somewhat stiff stellate hairs with arms to 0.8 mm long, the hairs nearest the distal end of the filament with arms predominantly pointing upward; anthers 5 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary short-stellate-pubescent; style glabrous. Fruit unknown.

Endemic to western Panama; 10–104 m; forests. Flowering (in bud only): July, August.

Styrax panamensis is known with certainty only from the type collection. Its occurrence in low-elevation tropical forest habitat is unusual with respect to the other *Styrax* species treated in this revision. Fruiting specimens from 1550 to 1650 m elevation in the Serranía del Darién [*Gentry & Mori 13797* and *14073* (MO)] might belong to this species, but they have smaller leaves with long-acuminate apices. A fruiting specimen from 150 m elevation in Mpio. de Hidalgotitlán, Veracruz, Mexico (17°15′45″N, 94°29′30″W, *Wendt 3576*), also may be this species. More material, particularly good flowering and fruiting material of plants from near Pittier's collection site, as well as material at anthesis from the Darién region and the locality at Veracruz will be required to better understand *Styrax* in these areas.

Although only flower buds are available on the type, careful analysis of internal floral morphology suggests that *S. panamensis* is allied to other lowland South American species (e.g., *S. guianensis*) that lack auricles but possess a dense mass of hair with relatively long arms (> 0.7 mm) on the ventral side of the stamen filaments.

Perkins apparently did not see the Pittier collection. Gonsoulin (1974) annotated it as *Styrax argenteus* var. *ramirezii* (= *S. argenteus* var. *micranthus*; see comments under *S. ramirezii*).

13. Styrax peruvianus Zahlbr., Ann. K. K. Naturhist. Hofmus. 7: 4. 1892. TYPE: Peru. Cajamarca: Tambillo, *Jelski 16* (holotype, W; isotypes, B destroyed, photo in F, GH, MICH, MO, NY). Figures 13, 36–39, 47.

Evergreen tree to 10 m. Young twigs lepidote, the scales brown mixed with olive-green; outer layer of older twigs not exfoliating. Petiole (7–)10–15 mm long. Lamina thick-chartaceous, 6.5–12 × 2.2–5 cm, 2.0–3.1 times as long as wide, lance-

elliptic or oblanceolate, secondary veins 7–9; apex abruptly short-acuminate to rarely acuminate; base cuneate to slightly attenuate, symmetric or slightly oblique; adaxially glabrous or sparsely lepidote; abaxially covered (surface and veins) with olive-green peltate or lacerate-margined scales, and more scattered orange-brown scales; margin entire. Inflorescences racemose, axillary or false-terminal, 3.5–8.5 cm long, 3–9-flowered. Lower pedicels 8–14 mm long. Calyx 3–3.5 × 4.5 mm, cupuliform, olive-green lepidote with scattered light orange-brown scales, scales 0.27–0.44 mm diam., peltate or lacerate-margined; calyx teeth 5, to 0.5 mm long, deltoid; calyx margin slightly concave or rarely truncate between the teeth, inner margin often glandular. Corolla pink, 10–16 mm long, petals connate 1–3 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 7–10 × 1.8–3.2 mm, non-overlapping, spreading to recurved, linear-deltoid, thickened, vesture on the outer distal third of the lobes consisting of peltate or lacerate-margined scales. Free portion of stamen tube 1–1.7 mm long; distinct portion of filament 1.5–2.0 mm long, of equal width throughout; ventrally with prominent auricles bearing radiate scales or stellate hairs with arms 0.1–0.3 mm long, glabrous elsewhere; anthers 4–5.5 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary lepidote; style glabrous or pubescent at base only; stigma 0.3–0.4 mm wide. Drupe 11–20 × 5–10 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Northwestern Costa Rica to western Panama; also Colombia, Ecuador, and Peru; 1600–2100 m; lower montane rainforests, mixed forests; found on windswept ridges and in forest understory. Flowering: July–August; fruiting: January, June, October.

Additional specimens examined. COSTA RICA. **Alajuela:** Monteverde Reserve, El Valle Trail near continental divide, *Haber ex Bello 3173* (MO). **Guanacaste:** Parque Nacional Guanacaste, Fila Orosilito, *I INBio 16* (CR, F, MO). **Puntarenas:** Monteverde Reserve, Senderos Chomogo and Pantanoso, *Haber & Zuchowski 9318* (CR, INB). PANAMA. **Chiriquí:** Cerro Colorado, along mining road 31.6 km beyond bridge over Río San Félix, *Croat 37190* (MO, NY); Cerro Pate Macho, *de Nevers & McPherson 6848* (CAS, MO).

Styrax peruvianus is easily distinguished from other sympatric species by the peltate or lacerate-margined scales on the leaves, branches, and inflorescences. The only other species in the region with this feature is *S. conterminus,* which has narrowly elliptic leaves, non-auriculate stamen filaments, and non-tapered anther sacs.

This species has been only rarely collected throughout its range. The description given here is based on the specimens cited above and the following: *L. Ellemann 66559* (LOJA, QCA; Ecuador), *G. Lozano C. 2537* (COL; Colombia), *R. Sandino-Pardo 11* (COL; Colombia), and *B. Wallnöfer 18-1588* (W; Peru). *Styrax peruvianus* is considered to belong to a lineage comprising several species in South America with peltate scales, stamen filaments with auricles and/or dense pubescence with long-armed hairs (> 0.8 mm) ventrally, and prolonged anther connectives, including *S. cordatus* and *S. leprosus.*

14. Styrax platanifolius Engelm. ex Torr., Smithsonian Contr. Bot. 6: 4. 1854 ["*S. platinifolium*"]. TYPE: U.S.A. Texas: Comal Co., near New Braunfels, 1851, *Lindheimer s.n.,* (holotype, MO; isotype, GH). Figures 55, 56, 65, 66.

Deciduous shrub multi-stemmed from the base, to 3 m. Young twigs glabrous to densely white-stellate-pubescent, sometimes somewhat glaucous, often toward the base with scattered orange-brown or dark brown stalked stellate hairs; outer distal layer of older twigs often exfoliating into long strips. Petiole 6–20 mm long. Lowest leaf pair on each twig usually alternate, sometimes subopposite. Lamina chartaceous, 4.5–9.0(–12) × 4.2–9(–11.5) cm, depressed-orbicular or very broadly ovate, sometimes slightly conduplicate, as evidenced by longitudinally folded laminae on herbarium specimens, secondary veins 5–6; apex rounded or obtuse, rarely acute, sometimes broadly cuspidate; at least some leaf bases on each leaf cordate or truncate, others rounded, usually slightly attenuate, symmetric or slightly oblique; adaxially glabrous or pubescent; abaxially glabrous or thickly covered with white stellate hairs, with scattered, orange-brown or dark brown stalked stellate hairs especially prevalent on veins and the lowest pair of leaves on each shoot, the stellate portion often deciduous from the base, the secondary and tertiary veins evident but not prominent; margin usually eglandular, either entire or apically with 2–several lobes or coarse teeth. Inflorescences false-terminal, sometimes contracted and thus appearing umbellate, 2–5 cm long, 1–7-flowered. Lower pedicels 4–9 mm long, becoming wider from base to apex, 1.3–2.3 times as long as the calyx. Calyx 3–5(–6) × 4.5–5.5 mm, campanulate, glabrous or densely white-stellate-pubescent, margin and/or teeth at least sparsely glandular; calyx teeth 0–7, irregularly distributed, to 1 mm long, narrow-deltoid or linear, the calyx margin truncate between the teeth. Corolla white, 12–21 mm long, petals con-

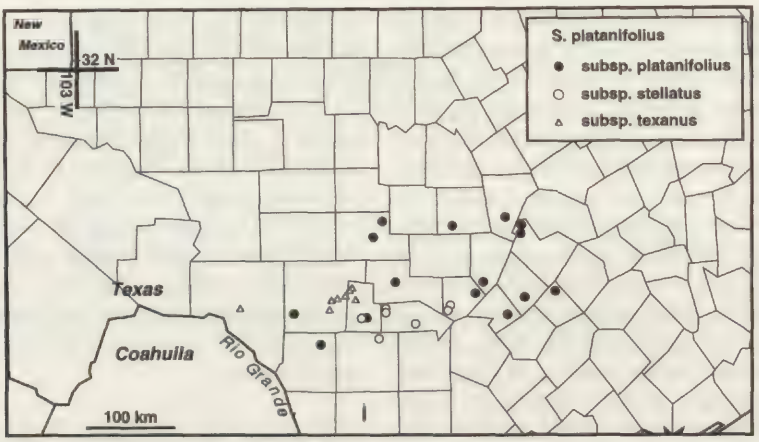


Figure 65. Distribution of *Styrax platanifolius* subsp. *platanifolius*, *S. platanifolius* subsp. *stellatus*, and *S. platanifolius* subsp. *texanus*.

nate up to the calyx margin distally; corolla lobes 5(6), imbricate in bud, 11–18 × 3–7 mm, overlapping, spreading, thin, elliptic, vesture on the outer distal third consisting of stellate hairs. Free portion of the stamen tube 1–6 mm long; distinct portion of filament 2–9 mm long, of equal width throughout, ventrally not auriculate and sparsely white-stellate-pubescent, becoming glabrous toward the distal end of the filament, the hairs with arms to 0.15 mm long; anthers 3–5.5 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely short-stellate-pubescent; style pubescent at base only to nearly throughout; stigma 0.3–0.7 mm wide. Capsule 7–10 × 7–11 mm (broader when 2–3-seeded), globose, 3-valve-dehiscent, the wall hard, stellate-canescent, smooth but usually transversely wrinkled post-dehiscence. Seeds 6–9.5 mm long; seed coat glabrous.

West-central Texas on the Edwards Plateau escarpment and in the Davis Mountains, to Coahuila and Tamaulipas, Mexico, where it exists along the

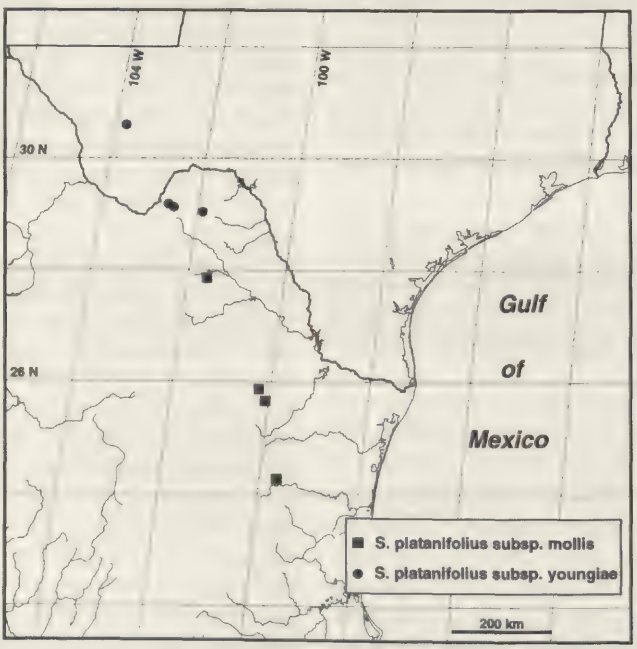


Figure 66. Distribution of *Styrax platanifolius* subsp. *mollis* and *S. platanifolius* subsp. *youngiae*.

Table 1. Characters differentiating *Styrax platanifolius* from *S. redivivus* (modified from Fritsch, 1996b).

Character	*S. platanifolius*	*S. redivivus*
larger undehisced capsules	7–10 mm long	11–15 mm long
larger seeds	6–9.5 mm long	9.5–12 mm long
mature capsule pubescence	canescent	tawny or fulvous
pedicel/calyx length (ratio)	1.3–2.3	0.5–1.4
calyx	3–5 (–6) × 4.5–5.5 mm	4–7 × 5–7 mm
leaf margins	often coarsely lobed or irregularly undulate	never lobed

northeastern escarpment of the Sierra Madre Oriental, and the Chihuahuan desert mountains; 200–2000 m; dry wooded bottomlands, rocky stream banks and ledges, wooded canyons, izotal vegetation; found on limestone, and according to Cory (1943), igneous soil in the Davis Mountains.

After publication of *S. platanifolius* (Torrey, 1853), no new *Styrax* taxa from Texas were published until Cory (1943) described two new species (*S. texanus* and *S. youngiae*) and one new variety (*S. platanifolius* var. *stellatus*) from the Edwards Plateau and the Davis Mountains. Gonsoulin (1974) agreed completely with Cory's assessment of the genus in Texas and incorporated material collected in northern Coahuila and not seen by Cory into *S. youngiae*.

Data from morphology (Fritsch, 1996b), isozymes (Fritsch, 1996a), and DNA sequences (Fritsch, 1995) strongly suggest that these taxa are more closely related to each other than to other taxa of *Styrax*. However, in my opinion the morphological variation within and among these taxa warrants the recognition of only one species of *Styrax* from Texas. Cory (1943) and Gonsoulin (1974) presented a summary table of differences among *S. platanifolius, S. texanus,* and *S. youngiae*. Most of the characters in this summary (i.e., upper leaf surface color, calyx color, presence of calyx glands, vein reticulation on lower leaf surface) are not taxonomically reliable upon close inspection of the collections. The remainder involve differences in the quantity of pubescence on the vegetative parts, pedicels, and calyces that I consider to be taxonomically inconsequential within many other species of *Styrax*, such as *S. glabrescens, S. grandifolius,* and *S. redivivus*. To place this variation in perspective, there are reliable characters separating members of this group from the closely related species *S. redivivus*, endemic to California (Fritsch, 1995, 1996b; Table 1).

Additional evidence for the recognition of only a single species of *Styrax* from Texas comes from isozyme analysis (Fritsch, 1996a). Pairwise genetic identities (*I*) estimated from isozyme allelic variation between populations of *S. platanifolius* subspp. *texanus* and *stellatus* range from 0.986 to 0.991, which is within the 0.90–1.00 range expected among infraspecific taxa (Crawford, 1983). In contrast, pairwise estimates of *I* between populations of *S. redivivus* from California and all taxa from Texas sampled is 0.446, well below the reported average among congeneric species (0.67; Gottlieb, 1977; Crawford, 1983, 1989). Because only four populations within *S. platanifolius* were sampled, it would be desirable to obtain more isozyme data from additional populations, especially for subspecies *platanifolius, youngiae,* and *mollis*. In this regard, one individual sampled of subspecies *mollis* (= *S. youngiae* in Fritsch, 1996a) exhibited several alleles not shared by any individuals of subspecies *stellatus* or *texanus* (= "*S. platanifolius stellatus*" and "*S. texanus*" in Fritsch, 1996a, respectively).

Although the variation present is not considered sufficient to confer species status to *Styrax texanus* and *S. youngiae*, an argument can be made for retaining these taxa as subspecies within *S. platanifolius*. Variation in pubescence quantity in other New World species of *Styrax* is either not at all or only poorly associated with geography, ecology, or life history (*S. glabrescens, S. grandifolius*), or at most is distributed along latitudinal clines (*S. americanus, S. redivivus*), and I do not recognize infraspecific taxa within these species. In contrast, trichome morphology or abundance within *S. platanifolius* is distinctly regional and facilitates the delimitation of nearly or completely allopatric taxa. Therefore, I have recognized five subspecies within *S. platanifolius* based on minor but distinctive differences. Trichome characters are those most reliable for the delimitation of these subspecies; characters of secondary importance include leaf form, calyx gland density, and surface features of the stem.

Gonsoulin (1974) incorrectly attributed the description of *S. platanifolius* to "Boston J. Nat. Hist. 6: 146–147, 1854." The article to which I presume he was referring (Gray, 1850) is the second of a three-part account of F. Lindheimer's collections in

western Texas. Because it covers the collections from the years 1845–1848, this article would not be expected to list the 1851 *S. platanifolius* collection in any case. The other two parts to the series (Engelmann & Gray, 1845; Blankinship, 1907) also do not cite the collection.

KEY TO THE SUBSPECIES OF *STYRAX PLATANIFOLIUS*

1a. Abaxial laminar surface glabrous or visible through the pubescence.
  2a. Leaves, pedicels, and calyces without white stellate hairs ..... 14a. *S. platanifolius* subsp. *platanifolius*
  2b. Leaves, pedicels, and calyces with white stellate hairs.
    3a. Longest arms of each stellate hair on the abaxial laminar surface typically about 0.8 mm long, often exceeding 1 mm; laminar surface soft to the touch; calyx teeth to 0.3 mm long, the calyx margin sparsely glandular ..... 14b. *S. platanifolius* subsp. *mollis*
    3b. Longest arms of each stellate hair on the abaxial laminar surface typically about 0.4 mm long, rarely if ever reaching 1 mm; laminar surface somewhat rough to the touch; calyx teeth to 1 mm long, the teeth and calyx margin densely glandular 14c. *S. platanifolius* subsp. *stellatus*
1b. Abaxial laminar surface completely covered and obscured by the pubescence.
  4a. Young twigs faintly glaucous; abaxial laminar surface, pedicels, and calyces with a thin and even layer of white stellate pubescence; adaxial laminar surface glabrous; style pubescent from base to ca. 15–35% of the total length ..... 14d. *S. platanifolius* subsp. *texanus*
  4b. Young twigs stellate-pubescent; abaxial laminar surface, pedicels, and calyces with a thick layer of white stellate pubescence; adaxial laminar surface stellate-pubescent; style pubescent from base to ca. 60–80% of the total length ..... 14e. *S. platanifolius* subsp. *youngiae*

14a. Styrax platanifolius subsp. **platanifolius.** Figure 65.

Young twigs glabrous except for scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina glabrous on both sides except for scattered orange-brown or dark brown stalked stellate hairs abaxially on some leaves, margin often irregularly undulate, weakly 3-lobed, or coarsely toothed, less often entire. Pedicel and calyx glabrous. At least some calyx teeth to 1 mm long, the teeth and calyx margin densely glandular. Style pubescent from base to 15–35% of the total length.

Rare, occurring in west-central Texas on the Edwards Plateau escarpment; 200–700 m; dry wooded bottomlands, rocky banks and ledges. Flowering: April–May; fruiting: July–September.

Common name. Sycamore-leaf snow-bell (Gonsoulin, 1974).

Additional specimens examined. UNITED STATES. **Texas:** County unknown: San Marcos and vicinity, summer 1897, *Stanfield s.n.* (NY); Bull Cr., Mr. J. Beard's place, 14 Apr. 1915, *Young s.n.* (TEX). Blanco Co.: Little Blanco River near intersection of Hwy. 281 and 473, *Dorr & Nixon 1910* (NY); bluff overlooking Little Blanco River, S of Twin Sisters, *Gonsoulin 1289* (NY); Little Blanco River and Hwy. 66–281, 24 Aug. 1947, *Parks s.n.* (LL); intersection of Hwy. 281 and 473 on N bank of Little Blanco River, 29 Apr. 1972, *Welborn & Sanstrup s.n.* (TEX). Burnet Co.: 3 mi. N of Smithwick, *Henry 6557* (GH); 12 mi. WSW of Bertram, 16 June 1950, *Tharp s.n.* (TEX). Caldwell Co.: ca. 4.5 mi. W of Delhi on TX 713, *Gonsoulin 1287* (NY). Edwards Co.: ravine near W Nueces River, ca. 19 mi. SW of Rocksprings, *Gonsoulin 1306* (NY). Hays Co.: near Lake Travis, 9.3 mi. WNW of Cedar Creek, *Gonsoulin 1288* (NY). Kendall Co.: near Edge Falls along Curry Creek, *Correll 29152* (GH, LL); below Edge Falls, ca. 5 mi. S of Kendalia, *Correll & Smith 29572* (GH, LL); Edge Falls, *Correll & Correll 37024* (LL). Kerr Co.: near Guadalupe River, ca. 4 mi. W of Hunt, *Gonsoulin 1305* (NY). Kimble Co.: one half mi. E of Junction near Hwy. 290, 18 May 1960, *Coleman s.n.* (TEX); Junction, *Palmer 10907* (A); Big Saline Creek, *Reverchon 1551* (GH). Kinney Co.: on banks of Nueces River, *Gonsoulin 1307* (NY). Llano Co.: Enchanted Mountain, 26 June 1932, *C. E. A. s.n.* (TEX); Enchanted Rock, *Jermy s.n.* (NY), *Jermy 105* (MO), 12 June 1930, *Whitehouse s.n.* (GH, NY), 25 Apr. 1931, *Whitehouse s.n.* (TEX), 16 Aug. 1931, *Whitehouse s.n.* (TEX). Real Co.: ca. 4.5 mi. E of Leaky on TX 337, *Gonsoulin 1308* (NY). Travis Co.: cultivated at 1405 Rabb Rd. in Austin, *Correll & Correll 37003* (LL); Austin, Apr. 1913, *Huppetz s.n.* (TEX); Travis Peak, Austin, 3 May 1930, *Prowse s.n.* (TEX), 3 May 1930, *Whitehouse s.n.* (GH); near Austin, *Wright s.n.* (GH).

This is the most widespread of the three subspecies of *Styrax platanifolius* endemic to Texas, but it is extremely rare throughout its range. Populations apparently were larger and more common in the early 1900s, but the subspecies has since declined dramatically (Cory, 1943; J. Poole, Texas Parks and Wildlife Department, Austin, Texas, pers. comm.; pers. obs.). Many populations have been extirpated, and those that remain often consist of only a single individual or a few plants. Documentation and monitoring of remaining populations, assessment of genetic variation among all remaining individuals, and management plans are desperately needed to ensure the survival of members of this subspecies.

14b. Styrax platanifolius subsp. **mollis** P. W. Fritsch, subsp. nov. TYPE: Mexico. Coahuila: Mpio. de Muzquiz, Rancho Agua Dulci, E slope of the Sierra de San Manuel, 28 June 1936, *F. L. Wynd & C. H. Mueller 340* (holotype, MO; isotypes, A, MICH, NY). Figure 66.

Lamina alba-stellata-pubescens utrinque, subtus ad tactum mollis, brachis longissimis pilorum stellatorum typice 0.8 mm longis, saepe excedentibus 1 mm longis, pagina abaxiali visibili infra tomento; *pedicelli* albi-stellati-pubescentes; *calyx* alba-stellata-pubescens, margine inferme glandifero, dentibus usque ad 0.3 mm longis.

Young twigs densely white-stellate-pubescent in addition to scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above with scattered stellate pubescence, the hairs most often simple, sometimes stellate and then to about 4-armed, below moderately densely white-stellate-villous in addition to scattered orange-brown or dark brown stalked stellate hairs on some leaves, soft to the touch, the surface visible through the pubescence, the longest arms of each stellate hair typically about 0.8 mm and often exceeding 1 mm long, margin often usually entire, less often weakly undulate. Pedicel and calyx with white stellate hairs of variable length. Calyx teeth to 0.3 mm long, the calyx margin sparsely glandular. Style pubescent from base to 30–75% of the total length.

Rare, Coahuila and Tamaulipas, Mexico, along the eastern escarpment of the northern extension of the Sierra Madre Oriental and Chihuahuan desert mountains; 1200–1400 m; wooded canyons. Flowering: April.

Additional specimens examined. MEXICO. **Nuevo León:** Monterrey, Chipinque, *Peterson 1243* (TEX); Monterrey, La Silla Trail, *Smith M149* (TEX).

I have also seen individuals of this subspecies cultivated at the Berkeley Botanic Garden, Berkeley, California (accession number 91.1305), originally collected by J. Fairey (Yucca Do Nursery, Waller, Texas) from Purificación, Tamaulipas, Mexico.

Styrax platanifolius subsp. *mollis* is a rare endemic to Coahuila and Tamaulipas, Mexico. It is the southernmost of the five subspecies recognized in *S. platanifolius,* having no apparent range overlap with the nearest subspecies to the north (subsp. *youngiae*), from which it is distinguished by the soft pubescence that does not completely cover the lower laminar surface. The distinctness of this subspecies from subspecies *youngiae* is highlighted by Gonsoulin's (1974) ambiguity regarding its identification. He cited the only specimen available to him of this subspecies (*Wynd & Mueller 340*) as *S. youngiae,* but annotated it as *S. platanifolius* var. *stellatus,* probably because subspecies *stellatus* resembles subspecies *mollis* more closely than does subspecies *youngiae.*

14c. Styrax platanifolius subsp. **stellatus** (Cory) P. W. Fritsch, comb. et stat. nov. Basionym: *Styrax platanifolius* var. *stellatus* Cory, Madroño 7: 111. 1943 ["*S. platanifolius* var. *stellata*"]. TYPE: U.S.A. Texas: Bandera Co., Sabinal Canyon, 16 June 1940, *V. L. Cory 34765* (holotype, A; isotype, NY). Figure 65.

Young twigs sparsely white-stellate-pubescent in addition to scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above with scattered stellate pubescence, the hairs with 6–14 arms, below with scattered white stellate pubescence in addition to scattered orange-brown or dark brown stalked stellate hairs on some leaves, somewhat rough to the touch, the surface visible through the pubescence, the longest arms of each stellate hair typically about 0.4 mm long, rarely if ever reaching 1 mm, margin often irregularly undulate, weakly 3-lobed, or coarsely toothed, less often entire. Pedicel and calyx with white stellate hairs of variable length. At least some calyx teeth to 1 mm long, the teeth and calyx margin densely glandular. Style pubescent from base to 50–70% of the total length.

Rare in west-central Texas on the Edwards Plateau escarpment; 500–700 m; dry wooded bottomlands, rocky banks and ledges. Flowering: April–May; fruiting: July–September.

Common name. Hairy sycamore-leaf snow-bell (Gonsoulin, 1974).

Additional specimens examined. UNITED STATES. **Texas:** Bandera Co.: 1 mi. N of Vanderpool, 15 June 1940, *Cory s.n.* (GH); Sabinal Canyon, 6.5 mi. N of Vanderpool, *Cory 34763* (TEX); Can Creek, 7 mi. N of Vanderpool, *Cory 49453* (LL), *Cory 49454* (A); Sabinal River, 7.5 mi. N of Vanderpool, *Henry 6560* (GH); steep ravine 9 mi. W of Boerne, *Johnson & Webster 599* (TEX); Upper Seco Creek, *Palmer 10237* (GH); Vanderpool, *Palmer 11528* (GH, MO, NY, POM); 2 mi. N of Vanderpool, *Parks 1009* (A); Vanderpool, *Parks 1942* (TEX), *Parks 40988* (A); Lost Maples State National Area, along the Sabinal River, *Poole & Watson 1205* (LL); Sabinal Canyon State Park, *Riskind & Snyder 1682* (LL, MO); Lost Maples State Natural Area, Hales Hollow, *Smith 517* (LL, NY); Lost Maples State National Area, drainage 15 of Sabinal River, *Smith 678* (LL); Lost Maples State National Area, *Snyder 274* (LL); Sabinal Canyon, ca. 7 mi. N of Vanderpool, 8 Apr. 1972, *Welborn s.n.* (TEX); Hwy. 407 (470?) between Utopia and Tarpley, S bank of Hondo Creek, 9 Apr. 1972, *Welborn s.n.* (TEX). Kendall Co.: ca. 6.5 mi. NW of Boerne, on tributary of Cibolo Creek, 24 Sep. 1983, *Breckenridge s.n.* (TEX); Spanish Pass, 5 July 1911, *Clemens & Clemens s.n.* (MO, POM, TEX); Boerne, 1911, *Hastings s.n.* (A); Boerne, *Palmer 9843* (GH, MO); Cibolo Creek, Boerne, *Palmer 11474* (GH, MO, NY); Cibolo, 15 June 1913, *Schattenberg s.n.* (A). Real Co.: along TX 337, 3 mi. W of Leakey, *Miller et al. 5145* (MO). Uvalde Co.: Garner State Park, SE boundary of park along Frio River,

Riskind 1691 (LL); Garner State Park, southern portion of park, 9 Apr. 1972, *Welborn s.n.* (TEX).

The range of *Styrax platanifolius* subsp. *stellatus* is contiguous with the southern boundary of subspecies *platanifolius*, occurring at the southern edge of the Edwards Plateau. It is rare throughout its range, with the exception of Sabinal Canyon State Park, where apparently populations are common and often composed of many individuals (*Riskind 1682*).

Gonsoulin (1974) incorrectly cited the holotype at TEX and an isotype at F.

14d. Styrax platanifolius subsp. **texanus** (Cory) P. W. Fritsch, comb. et stat. nov. Basionym: *Styrax texanus* Cory, Madroño 7: 112. 1943 ["*S. texana*"]. TYPE: U.S.A. Texas: Edwards Co., Polecat Creek, 4 July 1941, *V. L. Cory 34940* (holotype, GH). Figure 65.

Young twigs faintly glaucous, glabrous except for scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above glabrous, below thinly and evenly white-stellate-pubescent except for scattered orange-brown or dark brown stalked stellate hairs on some leaves, the surface completely covered and obscured by the pubescence, margin usually entire or weakly undulate, rarely lobed or coarsely toothed. Pedicel and calyx thinly and evenly white-stellate-pubescent. At least some calyx teeth to 1 mm long, the teeth and calyx margin densely glandular. Style pubescent from base to 15–35% of the total length.

Rare, occurring in west-central Texas on the Edwards Plateau escarpment; 500–700 m; steep limestone cliffs. Flowering: April–May; fruiting: July–September.

Common name. Texas snow-bell (Gonsoulin, 1974; Cox, 1987).

Additional specimens examined. UNITED STATES. **Texas:** Edwards Co.: Cedar Creek, canyon walls above perennial springs, 25 Sep. 1983, *Breckenridge s.n.* (TEX); Polecat Creek, 4 July 1940 or 1941, *Cory s.n.* (GH, RSA), 19 Apr. 1942, *Cory s.n.* (GH, POM), *Cory 34937* (TEX), *Cory 34938* (POM), *Cory 34939* (TEX); Cedar Creek, 1.25 mi. above Roberts Creek, *Cory 37767* (TEX), *Cory 37769* (A); Cedar Creek, *Cory 38763* (TEX), *Cory 38764* (A); Polecat Creek, *Cory 38933* (TEX); Polecat Canyon, *Cory 38934* (NY); Little Hackberry Canyon, *Cory 42953* (NY); Little Hackberry Creek, 14.5 mi. E of Rocksprings, *Cory 42956* (TEX); Polecat Creek, *Cory 49179* (LL); cliff above Cedar Creek, NW of Barksdale, *Dorr & Nixon 1918* (TEX); Cedar Creek Canyon NW of Barksdale, *Johnston et al. 7428* (TEX); Jessup Ranch on Little Hackberry Creek, *Keeney 1456* (NY); Polecat Creek, *Keeney 1457* (MO). Real Co.: Nueces Canyon, 4.5 mi. N of Hackberry, *Cory 42659* (F), *Cory 42661* (TEX), *Cory 42664* (NY), *Cory 42666* (TEX); Nueces River, 4.25 mi. above Hackberry, *Cory 42668* (A), *Cory 42669* (POM); Nueces River, 1 1/3 mi. above Hackberry, *Cory 42673* (A), *Cory 42677* (NY), *Cory 42678* (F); 9 mi. ENE of Vance, W side of Bullhead Creek, *Johnston 7304* (TEX).

Styrax platanifolius subsp. *texanus* has the narrowest distribution of the five *S. platanifolius* subspecies, with documented localities in Edwards and Real Counties, Texas, and one population reported in Del Rio County, Texas. It is probably also the rarest of the subspecies, with only nine populations known, four of which consist of more than two individuals (J. Poole, Texas Parks and Wildlife Department, Austin, Texas, pers. comm.). Although seed production and the germination rate of *S. platanifolius* subsp. *texanus* are relatively high, grazing by both native and exotic herbivores has prevented regeneration within populations (Cox, 1987). Recovery efforts by the Texas Parks and Wildlife Department are under way to help ensure the survival of this taxon.

Gonsoulin (1974) incorrectly cited the type as "*Cory* 19 Apr 1942" with isotypes at GH and NY.

14e. Styrax platanifolius subsp. **youngiae** (Cory) P. W. Fritsch, comb. et stat. nov. Basionym: *Styrax youngiae* Cory, Madroño 7: 113. 1943 ["*S. Youngae*"]. TYPE: U.S.A. Texas: Limpia, canyon (on MO specimen only), Davis Mountains, 12 May 1914, *M. S. Young s.n.* (holotype, TEX; *M. S. Young 23* isotype, MO). Figures 55, 56, 66.

Young twigs densely white-stellate-pubescent in addition to scattered orange-brown or dark brown stalked stellate hairs toward the base. Lamina above with scattered stellate pubescence, the hairs with 6–14 arms, below with a thick layer of white stellate pubescence except for scattered orange-brown or dark brown stalked stellate hairs on some leaves, the surface completely covered and obscured by the pubescence, the hairs of variable length, margin entire, undulate, or coarsely toothed. Pedicel and calyx with a thick layer of white stellate pubescence, the hairs of variable length. Calyx teeth to 0.6 mm long, usually shorter, the teeth and calyx margin sparsely glandular. Style pubescent from base to 60–80% of the total length.

Rare, Davis Mts., Texas, and eastern slopes of Chihuahuan desert mountains in northern Coahuila; 900–2000 m; izotal vegetation (*Yucca, Nolina, Dasylirion* associates), piñon/juniper woodland, in canyons; found on limestone; according to Cory (1943), found on igneous substrates in the Davis Mts., Texas, but this needs confirmation. Flowering: April–May; fruiting: July–September.

Common name. Young's snowbell (Gonsoulin, 1974).

Additional specimens examined. MEXICO. **Coahuila:** 12 mi. E of Boquillas in Sierra del Carmen, *Henrickson 11499* (TEX), *Henrickson 11561* (TEX); 17 km N of Rancho, El Jardín, *Johnston et al. 11888* (CAS, F, LL, MO, NY); Mina El Popo, ca. 2 km S of Cañon El Diablo, *Johnston et al. 11925* (CAS, F, LL, MEXU, MO, NY); 1 km W of Rancho Lagunita, *Riskind & Patterson 1915* (TEX); Mpio. de Villa Acuña, Serranías del Burro, Rancho El Bonito, *Riskind 2079* (TEX); Sierra del Carmen, 1/2 mi. S from its junction with the main part of Cañón del Diablo, *Wendt et al. 148b* (TEX); Sierra del Carmen, in fork of Cañón del Diablo, *Wendt 582* (MEXU, TEX).

Styrax platanifolius subsp. *youngiae* occurs in the Davis Mountains, Texas, U.S.A., and the Sierra del Carmen and surrounding mountainous regions in the Chihuahuan Desert, Coahuila, Mexico. The type locality in the Davis Mountains ("Limpia; canyon") has not been rediscovered. The Davis range consists primarily of igneous substrates, so Cory (1943) presumed the type to have come from an igneous rather than a limestone substrate. This fact and the higher elevation at which this subspecies occurs were considered to be features that distinguish *S. youngiae* from *S. platanifolius* and *S. texanus*. However, all subsequent collections of *S. platanifolius* subsp. *youngiae* that indicate substrate have come from limestone, placing in doubt Cory's (1943) assumption of an igneous substrate for the type. The elevation difference is still a distinguishing feature, although it is not as wide as Cory reported: Cory described *S. platanifolius* (= *S. platanifolius* subspp. *platanifolius* and *stellatus*) and *S. texanus* (= *S. platanifolius* subsp. *texanus*) as occurring below 600 m, and *S. youngiae* (= *S. platanifolius* subsp. *youngiae*) as occurring above 1200 m; current estimates of elevation ranges (based on data from herbarium labels) are 200–700 m for subspecies *platanifolius, stellatus,* and *texanus* combined, and 900–2000 m for subspecies *youngiae.*

The holotype is without number, but the isotype (*Young 23*) is clearly part of the same collection as the holotype, as indicated by the identical dates, general locality, and stage of leaf development.

15. Styrax radians P. W. Fritsch, sp. nov. TYPE: Mexico. Jalisco: (Mpio. de) San Sebastián, Hacienda del Cura, Sierra Madre, 2 Jan. 1927, *Y. Mexía 1351* (holotype, CAS; isotypes, A, DS, F, GH, MICH, MO, NY, UNC not seen, US). Figures 25, 61–63.

Arbor sempervirens; *lamina* ovata-oblonga vel elliptica, interdum lanceolata vel suborbicularis, subtus alba-stellata-pubescens, ad tactum mollis, venis secundariis et tertiariis evidentibus; *calyx* stellata-pubescens; *corolla* alba, tenuis, petalis connatis usque ad marginem calycem, lobis in aestivatione valvatis, sub anthesi apertis, patentibus moderate vel late; *filamenta* staminum partibus distinctis 2.5–3.5 mm longis et ad margines ventrales pilis stellatis aequiliter dispersis instructa, aliter fere glabra ventraliter praeter ad apices, brachis pilorum plus minusve radiatis ex axibus centralibus; *connectivum* antherae loculos noncontractos non vel leviter superans; *stigma* 0.6–0.8 mm lata.; *drupae* longiores 9–13 × 5–7 mm.

Evergreen tree to 12(–20) m. Young twigs grayish white-stellate-pubescent, often mixed with tawny- or orange-brown stellate hairs; outer layer of older twigs not exfoliating. Petiole 9–17 mm long. Lamina chartaceous, (8.5–)11–15(–24) × 4–9(–11.5) cm, broadly ovate-oblong or elliptic, sometimes lanceolate or suborbicular, secondary veins 9–15; apex acute to rounded, rarely broadly cuspidate; base subrounded to rounded, rarely truncate, subcordate, or cuneate, often slightly attenuate, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute white stellate hairs and also larger, woolly, whitish hairs rendering the surface soft to the touch, the minute hairs absent from the primary through tertiary veins, thus rendering the vein surface easily visible, the soft larger hairs rarely absent; margin entire. Inflorescences axillary or false-terminal, racemose or especially the larger usually paniculate, the racemes or panicle branches 2–6 cm long, 2–14-flowered. Lower pedicels 3–8 mm long. Calyx 2.5–5 × 2.5–5 mm, cupuliform or conical-cupuliform, grayish green-stellate-pubescent, rarely also with scattered orange-brown stellate hairs; calyx teeth 5, to 0.4 mm long or absent, deltoid, the calyx margin truncate or sometimes concave between the teeth, inner margin often glandular. Corolla white, 5–15 mm long, petals connate up to the calyx margin distally; corolla lobes 5, valvate in bud, 4–14 × 1–3 mm, non-overlapping, moderately or widely spreading, thin, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 0–4 mm long; distinct portion of filament 2.5–3.5 mm long, of equal width throughout, ventrally not auriculate, ± densely white-stellate-pubescent at the incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.7 mm long; anthers 2–6 mm long, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style pubescent from base to 40–85% of the total length; stigma 0.6–0.8 mm wide. Drupe 9–13 × 5–7 (wider when 2-seeded) mm (not including occasional beak), ovoid or narrowly ellip-

soid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Most common in Nayarit and extreme western Jalisco, but also in southern Sinaloa, southern Mexico, northern Guerrero, and Oaxaca, Mexico; 400–1400 m; *Quercus* savannas, *Quercus-Pinus* forests, ecotones between subtropical deciduous forest and tropical subdeciduous forest, tropical subdeciduous forests, tropical deciduous forests; found often in valley bottomlands or barrancas. Flowering: November–June; fruiting: February–July.

Common names. Aguacatillo (Oaxaca, *MacDougall H156*), azagar (Jalisco, *Vázquez & Guzmán 4164*), azajar (Jalisco, *Cárdenas et al. 79, Robles et al. 813*), cortapico (Jalisco, *Mexía 1351*), levadura (Nayarit, *Gentry & Gilly 10863*), mamuyo (Jalisco, *Cuevas & Rosales 1876*), zajar (Jalisco, *Santana et al. 4776*).

Uses. Wood is used for ox yokes, plows, and other purposes where durable, tough wood is desired (Jalisco, *Mexía 1351*).

Additional specimens examined. MEXICO. **Guerrero:** Tlalchapa, *Aguirre 100-51* (MEXU). **Jalisco:** ca. 35 km E of Cabo Corrientes, *Anderson & Anderson 6109* (MICH); El Tuito, 11.5 km al NW del pueblo por el camino a Ixtlahuahey, *Ayala 678* (F, MO, NY); 14 km W of Villa de Purificación, *Bullock 2024* (CAS); Cuautitlán, 2 km NE of El Durazno, *Cárdenas et al. 79* (WIS); Cabo Corrientes, 15–78 km SW of Puerto Vallarta, *Cochrane et al. 11942* (WIS); new dirt road from San Sebastián W of La Estancia, *Cochrane et al. 12047* (WIS); Mpio. de Purificación, El Ocotillo, 10–12 km al NE de Purificación, *Cuevas et al. 709* (WIS); 4–6 km al NE de Casimiro Castillo, *Cuevas et al. 2391* (WIS); 4–5 km al W de Casimiro Castillo, *De Niz et al. 23* (WIS); gorge of the Río Horcones, 27 km by road S from Puerto Vallarta, *Dieterle 4023* (MICH); center of El Durazno, *Iltis et al. 389* (WIS); 2–7 km ENE of El Durazno, *Iltis et al. 459* (WIS); Ayotitlán, *Judziewicz et al. 5212* (WIS); 7.6 km al E de la carretera Puerto Vallarta, *Lott 2540* (CAS, MICH, MO); ca. 4 km al N de El Tuito, *Magallanes 1534* (MEXU, TEX); 6 km al NE de La Cuesta, *Magallanes 3432* (MEXU, MICH, MO); 10 km up road 2.5 km NW of town of El Tuito, *Mayfield et al. 1632* (TEX); foothills of Sierra de Manantlán (ca. 40 km SE of Autlán), *McVaugh 23250* (MICH); 3–6 km above (N of) La Cuesta, *McVaugh 23415* (MICH); valley of a stream 5 km N of El Tuito, *McVaugh 25492* (MICH); 3–10 km generally E on the road to Mina del Cuale, *McVaugh 26376* (MICH); San Sebastián, trail to Las Mesitas, *Mexía 1861* (CAS, US); Cuautitlán, 1–2 km al SW de Telcruz, *Nieves 411* (WIS); 6 km al NE de Telcruz, *Nieves 546* (WIS); Cerro Huehuentón, *Pérez 814* (NY); along hwy. from Puerto Vallarta S to Chamela at Río Horcones, *Plowman 14547* (F); Mpio. de Cuautitlán, Río Ayotitlán entre Ayotitlán y Chancol, *Ramírez & Alcocer 477* (WIS); 6.5–7.5 km al NE de Cuautitlán, *Robles et al. 813* (WIS); 11 km al NE de Cuautitlán, *Santana & Guzmán 3303* (WIS); La Astilla, 6 km al NW de Minatitlán, *Santana et al. 4776* (WIS); Mpio. de Talpa de Allende, camino de Talpa a Cuale, 4 km después de Talpa, *Vázquez 1195* (WIS); 1–2 km al E del Tecolote, El Tecolote, Casimiro Castillo, *Vázquez & Guzmán 4164* (WIS). **México:** Mpio. de Temascaltepec, Luvianos, *Hinton 5309* (A, F, RSA), *Hinton et al. 6193* (CAS, NY, RSA, US); Mpio. de Temascaltepec, Villaneda, *Hinton et al. 7410* (A, MO, U, US); 3 mi. W of Luvianos, *Moran 10161* (DS, RSA). **Nayarit:** Camichín de Juaja, *Calzada 17840* (RSA); 4 km al NE del poblado de Sta. María del Oro, *Calzada et al. 18805* (MICH); Hwy. 28 between Tepic and Jalcatlán at km 14–16, *Croat 45262* (CAS, MO); 3 km al SW del Izote, camino al Cuarenteño, *Flores & Ruenes 1907* (F, MO); 11 km al W de Jalcocotán, *Flores & Ramírez 2498* (MICH, MO); 11 km al NE del Izote, camino a Palapita, *Flores-Franco et al. 3344* (MICH); 8 to 10 mi. W of Tepic, *Gentry & Gilly 10485* (LL, MICH); 15 mi. S of Tepic along hwy. to Compostela, *Gentry & Gilly 10811* (LL, MICH); 15 mi. S of Tepic along road to Compostela, *Gentry & Gilly 10863* (LL, MICH); mountains 9 mi. N of Compostela, *McVaugh & Koelz 541* (MICH); ca. 10 road-mi. E of Jalcocotán on road to Tepic, *McVaugh 12100* (MICH); 3 km NW of El Ocotillo, *McVaugh 23515* (MICH); along dirt road to Cuarenteño, 2–10 km from El Izote, *Miller & Téllez 3140* (CAS, MO); ca. 3 mi. E of Jalcocotán, *Norris 14959* (MICH); Rancho de la Siempreviva, *Ortega 60* (A, US); 2 a 10 km de Mazatan, *Ramírez & Flores 894* (MICH, MO); La Escondida, 14 km al NE de Tepic, *Téllez 10282* (MO); km 9.5 de la terraceria al Cuarenteño, *Téllez et al. 10412* (MICH, MO); between Tepic and Ixtlán del Río, 14 Nov. 1953, *Templeton s.n.* (RSA), *Templeton 7000* (RSA); 2 km al NE del Izote, Cerro San Juan, *Tenorio et al. 15605* (MICH, MO, RSA); 68 km al NE de San Pedro Ixzcatán, *Tenorio et al. 16929* (MICH, MO); 3 km al S del Izote, *Tenorio et al. 16984* (MICH, MO); Volcán Sanganguey, Tepic, *Walker 73H07* (NY). **Oaxaca:** Mpio. de San Jerónimo Coatlán, 38.6 km al SW de San Jerónimo Coatlán, *Campos 3467* (MEXU); Arroyo Limón, San Vincente, Putla, *MacDougall H155* (F, NY); San Vincente, Putla, *MacDougall H156* (F, NY); vicinity of Concordia, Pochutla, *Makrinus 551* (US); Cafetal Concordia (Cerro Espino), *Reko 3642* (US); Mpio. de San Mateo Pinas, 2 km de Cafetitlan, *Saynes 1437* (MEXU). **Sinaloa:** Mesa Malqueson, Cerro Colorado, *Gentry 5164* (DS, F, MEXU, MICH, MO, NY, RSA); El Agua Colgada, San Ignacio, *Montes 714* (US); San Juan, *Ortega 4118* (US); Mazatlán, *Ortega 5082* (BH, US); La Copetona, Arriba de Guadalupe de Los Reyes, *Tenorio 8364* (RSA, TEX); San Juan 14 km al SE de San Ignacio, *Tenorio 8441* (RSA).

Styrax radians is a relatively common and widespread species, occurring at mid elevations along the western escarpment of the Sierra Madre Occidental and the southern slopes of the trans-Mexican volcanic belt in Mexico. It appears to be most common in the states of Jalisco and Nayarit. The species occurs in three disjunct areas: Sinaloa to southern Jalisco, northern Guerrero and the southern portion of the state of México, and southern Oaxaca. The disjunction between western Mexico and eastern Mexico is likely to be real rather than an artifact of inadequate collecting because numerous collections of *Styrax*, especially *S. ramirezii*, have been made in the intervening areas. Plants occurring in the eastern part of the range have leaves that are a little larger on average than those

in the west, but they are otherwise essentially indistinguishable. Some populations in western Mexico have extremely small flowers, but this is only an extreme form of a completely continuous character and cannot be used for the designation of infraspecific taxa.

Perkins apparently did not see any collections of this species. Gonsoulin (1974) considered the collections placed here in *S. radians* to fall within the range of morphological variation exhibited by *S. argenteus* var. *argenteus*. However, *S. radians* is easily distinguishable from *S. argenteus* by the non-tapered anther sacs, non-prolonged connectives, and stamen filaments that lack both auricles and stiff, long-armed, upward-pointing hairs ventrally. Furthermore, the ranges of the species overlap only in Oaxaca. *Styrax radians* can be distinguished from other sympatric species of *Styrax* by its evergreen habit, drupaceous fruit, stellate pubescence throughout, and corolla lobes that are united only to the calyx margin. Pubescence on the lower laminar surface, consisting of a short, dense tomentum and a longer tomentum soft to the touch, is usually a good character distinguishing sterile specimens of *S. radians* from *S. ramirezii*; in *S. ramirezii*, the lower laminar surface is usually at least somewhat rough to the touch. However, the soft tomentum is not always present in *S. radians*, and some specimens of the stellate form of *S. ramirezii* approach *S. radians* in this respect. In these cases, the lower elevation at which *S. radians* occurs (400–1400 m, usually below 1000 m) as compared to that of *S. ramirezii* (770–3100 m, usually above 1500 m) can aid in identification.

16. Styrax ramirezii Greenm., Proc. Amer. Acad. Arts 34: 568. 1899. *Styrax argenteus* var. *ramirezii* (Greenm.) Gonsoulin, Sida 5: 227. 1974. TYPE: Mexico. Morelos: Mountain canyons above Cuernavaca, 15 May 1898, *C. G. Pringle 6848* (holotype, GH; isotypes, A, BH, BR, F, MEXU, MO, NY, PH not seen, POM, US, W). Figures 3, 4, 8, 57, 67–70.

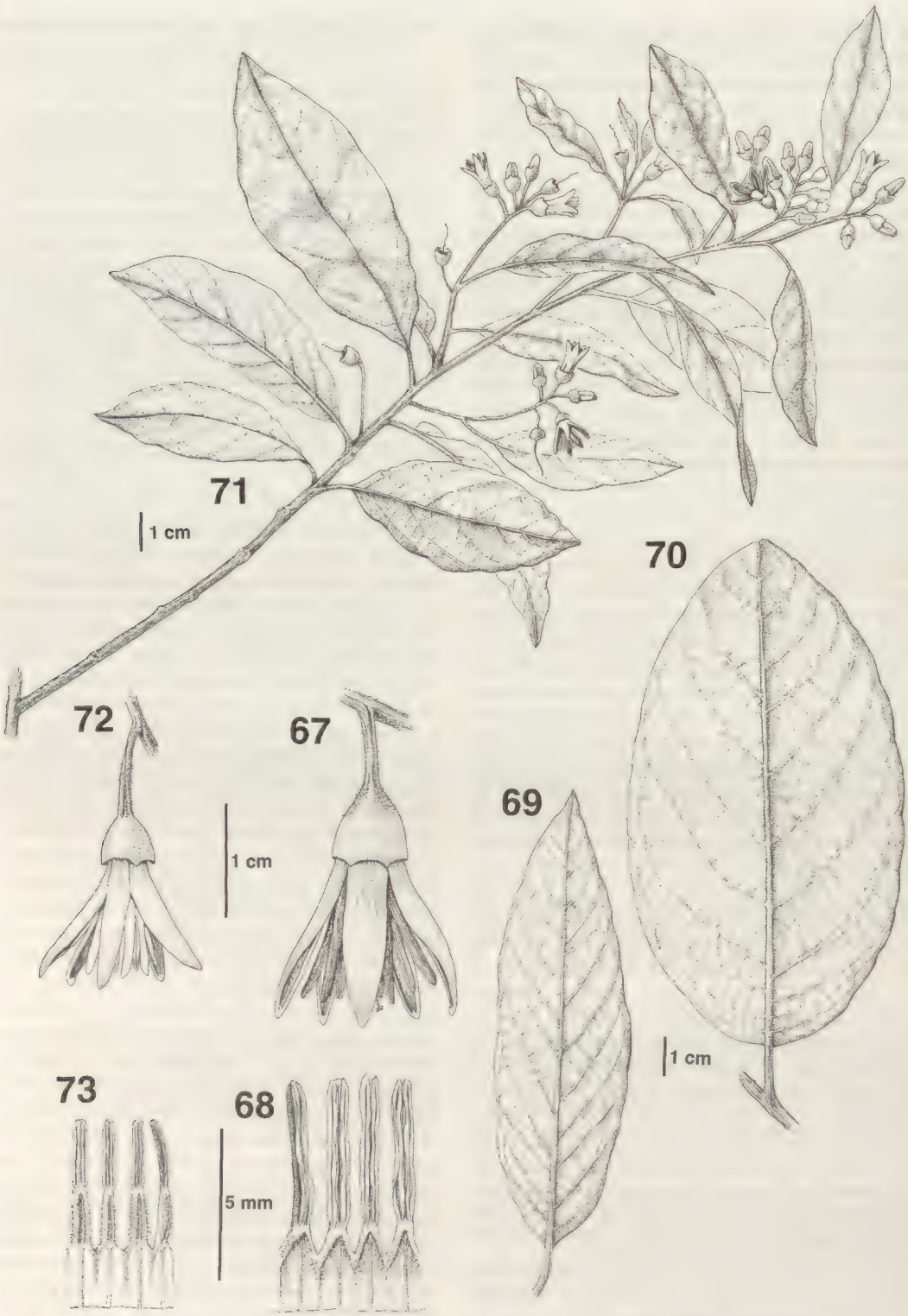
Styrax micranthus Perkins, Bot. Jahrb. Syst. 31: 480. 1902. *Styrax ramirezii* var. *micranthus* (Perkins) Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 54. 1907. *Styrax argenteus* var. *micranthus* (Perkins) D'Arcy, Ann. Missouri Bot. Gard. 66: 169. 1979. TYPE: Mexico. México: Temascaltepec, *Ehrenberg 498* (holotype, B destroyed; isotype, POM).

Styrax cyathocalyx Perkins, Repert. Spec. Nov. Regni Veg. 2: 24. 1906. TYPE: Mexico. Oaxaca: Rincón, May 1844, *H. Galeotti 1687* (holotype, B destroyed; photo of holotype, F, GH, US; isotypes, BR (2), G-DEL not seen, NY, US, W).

Styrax orizabensis Perkins, Repert. Spec. Nov. Regni Veg. 2: 25. 1906. *Styrax ramirezii* var. *orizabensis* (Perkins) Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 54. 1907. TYPE: Mexico. Veracruz (probably) or Puebla: Orizaba, 1856, *Botteri s.n.* or *1006* (holotype, B destroyed; isotypes, G-DC not seen, NY, W).

Styrax hintonii Bullock, Bull. Misc. Inform. Kew 1936: 9. 1936 ["*S. Hintoni*"]. *Styrax argenteus* var. *hintonii* (Bullock) Gonsoulin, Sida 5: 226. 1974. TYPE: Mexico. México: Dto. de Temascaltepec, Calera, 19 Apr. 1933, *G. B. Hinton 3798* (holotype, K; isotypes, F, GH, MO, US).

Evergreen tree to 20(–25–27) m. Young twigs short- to long-stellate-pubescent, or radiate-lepidote, the hairs yellow- or orange-brown, or dark brown, sometimes mixed with greenish gray hairs; outer layer of older twigs not exfoliating. Petiole 5–25 mm long. Lamina chartaceous, (10.1–)11.0–22.5 × 2.9–9.5(–10.5) cm, 1.6–4.4 times as long as wide, narrowly or broadly ovate-oblong, elliptic, or sometimes ovate, secondary veins 10–15; apex rounded to acuminate, sometimes emarginate through abortive tip development; base cuneate to rounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with greenish white stellate hairs of variable length or sometimes radiate scales, rarely nearly glabrous, the surface slightly to moderately rough or rarely soft to the touch, if soft then at least the lower third of the calyx villous; veins glabrous to densely tomentose; margin entire. Inflorescences axillary or false-terminal, racemose or sometimes paniculate, the racemes or panicle branches 2.5–12 cm long, (2–)5–17-flowered. Lower pedicels 4–11 mm long. Calyx (1.5–)3–6 × (3–)3.5–6.5 mm, cupuliform, grayish green- or brown-radiate-lepidote, or short- to long-stellate-pubescent; scales at mid-calyx (when present) 0.05–0.17 mm diam.; calyx teeth 5, to 0.5 mm long, deltoid, the calyx margin slightly or distinctly concave between the teeth, inner margin often glandular. Corolla white or pink, (8–)11–14 mm long, petals connate 1–3 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 6–10 × 2–3 mm, non-overlapping, slightly spreading, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of stellate hairs. Free portion of stamen tube 1–3 mm long; distinct portion of filament 0.6–2.0(–2.6) mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with arms to 0.3 mm long; anthers 3.0–4.8 mm long, 1.9–5.3 times as long as the distinct portion of the filaments, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style



Figures 67–73. 67–70. *Styrax ramirezii*. —67. Flower. *Pringle 9000* (MO). —68. Four adjacent stamens. *Hinton et al. 7605* (TEX). —69. Leaf of small-scaled form. *Pringle 9000* (MO). —70. Leaf of stellate form. *Koch & Sánchez 7929* (F). 71–73. *Styrax warscewiczii*. *Davidse 24632* (MO). —71. Flowering branch. —72. Flower. —73. Four adjacent stamens.

glabrous or pubescent at base only; stigma 0.3–0.5 mm wide. Drupe (7–)9–15 × 5–9 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Southern Sinaloa and Durango south to western Jalisco and northern Colima, east to northern Morelos and Oaxaca, and from the southern portion of the state of México south to central Guerrero; 770–3100 m; bosque mesofilo de montaña, *Quercus-Abies* forests, *Quercus-Pinus* forests, tropical semi-evergreen cloud forests, seasonally dry tropical subdeciduous forests; found often along waterways, sides of arroyos, humid canyons, deep riverbeds, disturbed situations, on granitic rock, rich soil, or sandy clay. Flowering: various times throughout year; fruiting: various times throughout year.

Common names. Azajar (Jalisco, *Niz et al. 290*), chilaquate (Morelos; Standley, 1924), escaramuza (Jalisco, *Mexía 1504*), garrapata (Michoacán, *Sharp 45499*), jaboncillo colorado (Michoacán, 17 Dec. 1971, *Rees s.n.*), mamullo (Jalisco, *Jardel et al. 214*), mamuyo (Jalisco, *Cuevas 1251, 1294,* and *1366*), memelita (Estado de México, *Hinton et al. 6145*), palo de casa (Jalisco, *Cevallos et al. 72, Muñoz & Vázquez 36*).

Additional specimens examined. Stellate form (selected specimens): MEXICO. **Guerrero:** Yesceros, *Hinton 14409* (GH, LL, RSA, US). **Jalisco:** San Sebastián, E of Arroyo Santa Gertrudis, *Méxia 1504* (A, CAS, DS, F, GH, MICH, MO, NY, US). **México:** Calera, Temascaltepec, *Hinton 7605* (A, DS, GH, LL, MICH, MO, RSA, TEX, US). **Michoacán:** Pontezuelas, 20 km al E de Morelia, *Rzedowski 18371* (DS, MICH, NY, TEX, US). **Nayarit:** base of Cerro Sanganguey, ca. 20 km SE of Tepic, *Miller 3114* (MO, TEX).

Large-scaled form: MEXICO. **Chiapas:** Paraje Vo'bits, *Laughlin 408* (DS, LL, US); 2 km camino Cabecera Zinacantan a pobablado Salinas, Zinacantan queda al W del pueblo, *Ton 9329* (CAS, TEX, WIS). **Oaxaca:** Dto. de Ixtlán, 6 km NNE of La Luz, *Boyle 3841* (MO); 20 km NE of Teotitlán del Camino, *Breedlove 59921* (CAS, NY); Mpio. de San Jerónimo Coatlán, 36 km al SE de Cruz de Honduras, *Campos 4740* (CAS, MEXU); Dto. de Cuicatlán, Cuyamecalco, *Conzatti 2338* (F); La Loma, Cuyamecalco, *Conzatti 2450* (F); 13 mi. E of Teotitlán, *Croat 48197* (MO); Mpio. de Comaltepec, S Comaltepec, *Hernández 322* (MEXU); Tonaguia, *Liebmann 596B* (F); Camino de Coyula a Cuyamacalco *Smith 347* (GH); Sierra Mazateca, Plan de Guadalupe, *Solheim 1397* (NY, WIS); 30 km al NE de Teotitlán, *Tenorio 14351* (MEXU, MO, RSA, TEX).

Small-scaled form (selected specimens): MEXICO. **Colima:** Mpio. de Minatitlán, Cerrito Breñoso, *Santana 2695* (MEXU). **Durango:** along the Mazatlán–Durango Hwy. 3–15 km toward El Salto from Sinaloa, *McVaugh 23593* (MICH). **Guerrero:** second ridge W of Petlacala, *Méxia 9059* (B, CAS, F, GH, LL, MO, NY, U, US). **Jalisco:** Rancho El Terrero, 1.5 km adelante del aserradero, *Flores 2680* (MEXU, TEX). **México:** 8 km al W de Cuernavaca, *Koch 7929* (CAS, F, MO, NY). **Michoacán:** San Felipe, Zitácuaro, *Hinton 11831* (F, GH, LL, MO, NY, US, W). **Morelos:** Sierra de Tepoxtlan, *Pringle 8023* (A, B, BH, BR, F, GH, MEXU, MO, NY, POM, US, W). **Sinaloa:** 1 mi. S of El Palmito on Hwy. 40, 1 mi. W of hwy., *Sanders 4405* (RSA, TEX).

Styrax ramirezii is one of the most common and widespread species treated in this revision. It is endemic to Mexico, occurring at relatively high elevations on the western slopes of the Sierra Madre Occidental from Sinaloa to Jalisco, the southern slopes of the trans-Mexican volcanic belt from Jalisco to Morelos, the Sierra Madre del Sur, the eastern escarpment of the Sierra Madre in Oaxaca, and rarely in the mountains of Chiapas. The distribution of this species shows a striking pattern along the trans-Mexican volcanic belt, essentially occurring only within a narrow band north of the Río Balsas basin.

This species exhibits a great deal of morphological variation across its range. The indumentum on the calyx can be of long or short stellate hairs, small or large radiate scales, or a mixture of these types. The pubescence on the lower laminar surface can consist of a thin to thick layer of long and/or short stellate hairs or radiate scales, or it may be nearly absent. The veins on the lower laminar surface are usually visible through any pubescence, but in most specimens from Oaxaca and Chiapas they are not. Scattered orange-brown stellate hairs or radiate scales sometimes occur on the calyx. Leaf and flower size varies a great deal throughout the range of the species.

Differences between *S. ramirezii* and other species of *Styrax* are addressed in the discussions under *S. argenteus, S. austromexicanus, S. magnus, S. radians,* and *S. warscewiczii.*

The extensive morphological variation exhibited by this species is often not random, either in terms of the correlations of characters or geographically, and this complexity is likely responsible for the contrasting treatments of *S. ramirezii* by Perkins (1907) and Gonsoulin (1974). Perkins (1907) defined *S. ramirezii* relatively narrowly, although her concept of this species was still broad enough to maintain three varieties within it (vars. *micranthus* and *orizabensis,* as well as the typical variety). She considered *S. cyathocalyx* and *S. warscewiczii* to be distinct species. Gonsoulin (1974), who had access to more material, considered the variation in most evergreen *Styrax* from Mexico as inconsequential or highly intergrading, and thus circumscribed *S. argenteus* var. *ramirezii* to include seven previously recognized taxa: *S. cyathocalyx, S. micranthus, S. orizabensis, S. polyanthus, S. polyneurus, S. ramirezii,* and *S. warscewiczii.* Gonsoulin (1974) consid-

Table 2. Mean and standard error (SE) of lamina length/width ratio (= l/w) and elevation for four groups within *Styrax ramirezii* recognized on the basis of calyx trichome differences. Measurements were obtained from herbarium specimens. Lamina shape was estimated by dividing length by width (average of two largest leaves per collection, one duplicate sampled per collection; sample list available from the author upon request). N = sample size.

Group	l/w			Elevation (m)		
	N	Mean	SE	N	Mean	SE
stellate form	43	2.19	0.06	39	1903	51
stellate/small-scaled intermediates	10	2.49	0.12	9	1977	107
small-scaled form	79	2.82	0.04	64	2193	122
large-scaled form	12	2.82	0.11	7	2289	40

ered *S. hintonii*, a species described subsequent to Perkins's published research on the Styracaceae, to be a variety of *S. argenteus*, and treated *S. magnus* and *S. vulcanicola*, also described after Perkins's publications, as synonyms of this variety.

The present revision follows Perkins's (1907) concept of *Styrax ramirezii* more closely than that of Gonsoulin (1974). The species status of both *S. ramirezii* and *S. warscewiczii* is recognized, as in Perkins (1907). However, in contrast with Perkins (1907), *S. cyathocalyx*, *S. ramirezii* var. *micranthus*, and *S. ramirezii* var. *orizabensis* are reduced to synonymy under *S. ramirezii*. The present treatment is concordant with Gonsoulin (1974) in that *S. cyathocalyx*, *S. micranthus*, and *S. orizabensis* are treated as synonyms, but differs in that *S. ramirezii* and *S. warscewiczii* are treated as species, and *S. polyanthus* and *S. polyneurus* are placed in synonymy under *S. argenteus* and *S. warscewiczii*, respectively. Furthermore, *S. argenteus* var. *hintonii* is placed here in synonymy under *S. ramirezii*, and *S. magnus* is treated as a distinct species; *S. vulcanicola* is treated as a synonym of the latter name.

The present circumscription of *S. ramirezii* comprises three fairly distinctive infraspecific entities. One of these has scales at mid-calyx that are 0.15–0.17 mm diam. This "large-scaled" form occurs only in Oaxaca and Chiapas. Another form has scales at mid-calyx that are 0.05–0.12 mm diam. This "small-scaled" form is wide-ranging, occurring from Sinaloa to northern Morelos and the Sierra Madre del Sur. In a third form the calyx is stellate-villous on at least the lower third. This "stellate" form is also widespread, but occurs entirely within the range of the small-scaled form, from Nayarit to the southern portion of the state of México and the Sierra Madre del Sur. Specimens exhibiting calyx-trichome morphology intermediate between that of the small-scaled and stellate forms comprise about 10% of the collections of *S. ramirezii*; most often they are from western Mexico and the state of México. Twig pubescence of the three forms generally corresponds to the calyx pubescence: the twigs are stellate-villous in the stellate form, and radiate-lepidote or rarely short-stellate-pubescent in the small-scaled and large-scaled forms. Also, most specimens of the large-scaled form possess a thick, dense layer of stellate hairs or radiate scales, whereas the other two forms have a thin layer of stellate hairs or radiate scales. In the stellate form this pubescence is often mixed with variable amounts of larger, white, stellate and somewhat stiff hairs. The small-scaled form is especially prevalent in northern Morelos, where the stellate form does not occur, and also extends farther north in western Mexico than the stellate form. The large-scaled form is apparently allopatric with respect to the other two forms. It is somewhat disjunctly distributed in the mountains of Oaxaca and a small area west of San Cristóbal de Las Casas. In this region *S. ramirezii* is difficult to distinguish from *S. warscewiczii* if flowers are not available.

The stellate form of *S. ramirezii* in general possesses more broadly elliptic leaves and occurs at lower elevations than the small-scaled and large-scaled forms (Table 2). Analysis of variance tests showed significant differences among means of the three groups (level = 0.05) for the length:width ratio and elevation ($P < 0.001$ for both). The small-scaled and large-scaled forms did not differ significantly for length:width ratio or elevation in a post hoc comparison. To assess the distinctness of these forms, canonical discriminant analysis was performed with the computer program SYSTAT (Systat, Inc.). In this procedure, the proportion of individuals classified correctly by the discriminant function reflects its ability to distinguish among groups (see, e.g., Murrell, 1994). Mahalanobis distances (Sneath & Sokal, 1973) among the groups were significant [all P (univariate and multivariate) < 0.001] and the three groups were identified correctly $^{44}/_{64}$ (68.8%), $^{5}/_{9}$ (55.6%), and $^{28}/_{39}$ (71.8%) of

the time, respectively, on the basis of the discriminant function. Thus, the discriminant function showed that calyx trichome type tends to be associated with leaf shape and elevation differences.

Despite this general correspondence, however, formal recognition of the forms of *S. ramirezii* at the infraspecific level is not warranted, mainly because reliable key characters are lacking and there is a relatively high proportion of small-scaled and stellate intermediate forms scattered throughout the range of the stellate form. Furthermore, in Jalisco and Nayarit intermediates seem to be of a different nature from those in other areas in that they possess short-stellate hairs and narrowly elliptic leaves (e.g., *Miller 3114, Téllez 10139*); other intermediates seem to have the calyx and leaf characters combined more or less independently (especially collections near Nanchititla, in the state of México, e.g., *Bartholomew 2914*). More detailed studies focusing on associations between morphological and molecular variation, as well as differences in elevation and habitat, would shed further light on the ecology and population genetics of these forms.

I have placed *Styrax cyathocalyx* in synonymy under *S. ramirezii* with some hesitation. Perkins (1907) maintained the two species on the basis of differences in the size of the flowers: 1 cm long in *S. cyathocalyx* and 1.5–2 cm long in *S. ramirezii*. *Styrax cyathocalyx* was based solely on *Galeotti 1687*. The duplicates that I have seen of this collection possess floral buds and no flowers at anthesis; presumably Perkins had mature flowers available to her, because she described the corolla as 1 cm long, whereas the longest buds I could measure were only 0.6 cm long. If Perkins's observation is correct, the corollas are unusually short for *S. ramirezii*. The calyx (2 mm long) is also short, especially relative to the unusually long pedicels (14 mm). Perkins (1906) also described the style as denticulate, but expressed uncertainty as to whether this was an artifact or real. In the specimens I examined, the style margins are entire, i.e., in no way do they differ from those of other specimens of *Styrax*. A fruiting specimen from the same area in Oaxaca (*Liebmann 596B*, Tonaguia, Oaxaca) shows the same calyx and pedicel characters, and the fruit is unusually small (7 × 5 mm) for *S. ramirezii*. It is therefore possible that these collections represent a distinct variety of *S. ramirezii*, or even a distinct species. More collections of evergreen *Styrax* from Oaxaca, especially in flower, are needed before a conclusive taxonomic decision regarding the status of *S. cyathocalyx* can be reached. It would be especially helpful to rediscover populations at sites where Galeotti and Liebmann collected.

Perkins (1902) listed only *Ehrenberg 498* in the protologue of *S. micranthus*; the location of original material was not precisely indicated. From the protologue of *S. ramirezii* var. *micranthus* in Perkins (1907) it can be inferred that this collection was deposited at B and/or W. Because no material of *Ehrenberg 498* occurs at W, however, it is reasonable to assume that the holotype was at B, and has been destroyed. The location of the original material of 15 species described in the publication that included *S. cyathocalyx* and *S. orizabensis* (Perkins, 1906) was indicated only vaguely as existing partly at B, BR, G-BOIS, G-DC, P, and/or W. I have assumed that the holotypes of these two species names were located at B, because that is where Perkins conducted her work; they have in all likelihood been destroyed. See the discussion under *S. glabrescens* for information concerning the collection date of *Galeotti 1687*.

When Gonsoulin (1974) made the combination *Styrax argenteus* var. *ramirezii*, he listed *S. micranthus* Perkins as a synonym. The latter name is the basis of *S. ramirezii* var. *micranthus* (Perkins) Perkins (1907), making Gonsoulin's varietal name superfluous. D'Arcy (1979) corrected Gonsoulin's error by making the combination *S. argenteus* var. *micranthus*.

The protologue of *Styrax ramirezii* Greenm. (Greenman, 1899) does not specify the holotype location. The NY duplicate of *Pringle 6848* is cited as the holotype of *S. ramirezii* in Gonsoulin (1974). However, Greenman worked at GH until 1899, studied at the University of Berlin from 1899 to 1901, and returned to GH in 1902 (Woodson, 1951). On this basis, I consider it best to regard the GH specimen as the holotype. Gonsoulin (1974) also cited the MO duplicate of *Hinton 3798* as the holotype of *S. hintonii*. However, Bullock worked at K, so the specimen there should be regarded as the holotype.

17. Styrax steyermarkii P. W. Fritsch, sp. nov. TYPE: Guatemala. Baja Verapaz: Unión Barrios, E of km 154, 16 Apr. 1975, *C. L. Lundell & E. Contreras 19214* (holotype, CAS; isotypes, LL, MEXU, MO, NY). Figures 6, 22–24, 47.

Arbor sempervirens; *lamina* 2.1–3.0plo longior quam latior, subtus pilis densis stellatis instructa; *calyx* radiatus-lepidotus, squamis densis cinerascentibus-viridis et saepe dispersis ferrugineis ad medicalycem 0.13–0.25 mm diam. instructus; *corolla* lobis in aestivatione valvatis, sub anthesi apertis, linearibus; *filamenta* staminum partibus distinctis ad margines ventrales auriculatis, auriculis pilis albis-stellatis dense instructis, brachis pilorum usque ad 1.5 mm longis, illis pilorum apicem versus pro parte

maxima ordinatis apicem floralibus versus; *antherae* 4.5 mm longae; *connectivum* antherae loculos contractos manifeste superans.

Evergreen tree to 20 m. Young twigs grayish green- to dark orange-brown-radiate-lepidote; outer layer of older twigs not exfoliating. Petiole 9–20 mm long. Lamina chartaceous, 11–16 × 3.5–7.5 cm, 2.1–3.0 times as long as wide, elliptic, secondary veins 6–8; apex acute to abruptly short-acuminate; base cuneate, rarely subrounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially covered with minute grayish green stellate hairs and sparsely scattered, larger, grayish green or orange-brown stellate hairs or radiate scales, the latter particularly prevalent near and on the veins; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 2.5–4 cm long, (1–)4–7-flowered. Lower pedicels 5–8 mm long. Calyx 2.5–3 × 4 mm, conical-cupuliform, in fruit shallowly cupuliform, grayish green-radiate-lepidote, sometimes with scattered orange-brown radiate scales toward the base; scales at mid-calyx 0.13–0.25 mm diam.; calyx teeth 5, to 0.3 mm long, linear, the calyx margin slightly concave between the teeth, inner margin often glandular. Corolla white, 12–15 mm long, petals connate up to the calyx margin distally; corolla lobes 5, valvate in bud, 10–12 × 2 mm, non-overlapping, spreading, slightly thickened, linear, vesture on the outer distal third of the lobes consisting of radiate scales. Free portion of stamen tube 1 mm long; distinct portion of filament 2–3 mm long, of equal width throughout, ventrally with auricles bearing a dense mass of stiff white stellate hairs with arms to 1.5 mm long, the hairs nearest the distal end of the filament with arms predominantly pointing upward, also pubescent below the auricles and at the sinus between adjacent filaments; anthers 4.5 mm long, the connectives distinctly prolonged beyond the tapered anther sacs. Ovary densely short-stellate-pubescent; style glabrous or pubescent at base only; stigma 0.3 mm wide. Drupe 16–18 × 9–11 mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens; fruiting calyx shallow, to 1.5 mm long. Seed coat glabrous.

In the mountains of Guatemala, departments of Baja Verapaz, Huehuetenango, and Suchitepéquez, and in the Cordillera Talamanca in Costa Rica; 1500(–2600?) m; "in high forest on top of hill" (*Lundell 19214*), riverbanks. Flowering: March, June, July; fruiting: April.

Additional specimens examined. COSTA RICA. **Puntarenas:** Buenos Aires, Ujarrás, Quebrada Dorora, *Herrera 5866* (CAS, CR). GUATEMALA. **Baja Verapaz:** Niño Perdido, *Lundell & Contreras 21219* (LL). **Huehuetenango:** Cerro Huitz, between Mimanhuitz and Yulhuitz, *Steyermark 48666* (F); Maxbal, ca. 17 mi. N of Barillas, *Steyermark 48848* (F). **Suchitepéquez:** Volcán Santa Clara, *Holdridge 2299* (US).

Styrax steyermarkii is rare in the high mountains of Guatemala and Costa Rica. It is named after Julian A. Steyermark (1909–1988), prolific collector of the Guatemalan flora, as well as that of Missouri and of Venezuela, who first found the species in 1942.

This species is similar to *Styrax glabratus* by virtue of its radiate-lepidote calyx and stiff, long-armed, upward-pointing hairs on the stamen filaments ventrally, but differs most obviously from this species in its densely pubescent, as opposed to nearly glabrous, lower laminar surface. Gonsoulin (1974) mistook *S. steyermarkii* for *S. argenteus* var. *ramirezii,* most likely because the lepidote calyx and general appearance are very similar to that of *S. warscewiczii,* which he had placed in synonymy under variety *ramirezii.* However, the flower buds on *Steyermark 48666* clearly exhibit the stiff, long-armed, upward-pointing hairs on the stamen filaments ventrally, which are absent in *S. warscewiczii,* and the leaves are larger.

The closest relatives of *S. steyermarkii* appear to be several species from Andean South America. These include *S. buchtienii* Sleumer, *S. ferax* J. F. Macbr., *S. heterotrichus* Perkins, *S. leptactinosus* Cuatrec., *S. pentlandianus* Remy, *S. socialis* J. F. Macbr., and *S. subheterotrichus* Herzog. The taxonomy and relationships of these species are uncertain, but their types share with *S. steyermarkii* the lepidote calyx and lower laminar surfaces that possess either stellate hairs throughout or a mixture of stellate and scale-like hairs. *Styrax steyermarkii* can be distinguished from all these species by the longer upward-pointing stellate hairs on the stamen filaments ventrally, and by the possession of narrower anther connectives. These species plus *S. steyermarkii* (= the *S. steyermarkii* group) appear to be allied to the *S. ovatus* group, i.e., those species with peltate or lacerate-margined scales covering the leaves, stems, and calyces (including *S. conterminus, S. cordatus, S. leprosus, S. ovatus,* and *S. peruvianus*). Some of the species in the *S. steyermarkii* group appear to be polymorphic for the strongly peltate scales represented by the *S. ovatus* group and the radiate-lepidote scales found within most individuals of the *S. steyermarkii* group. A clearer understanding of the taxonomy and phylogeny of these groups and their phylogenetic positions

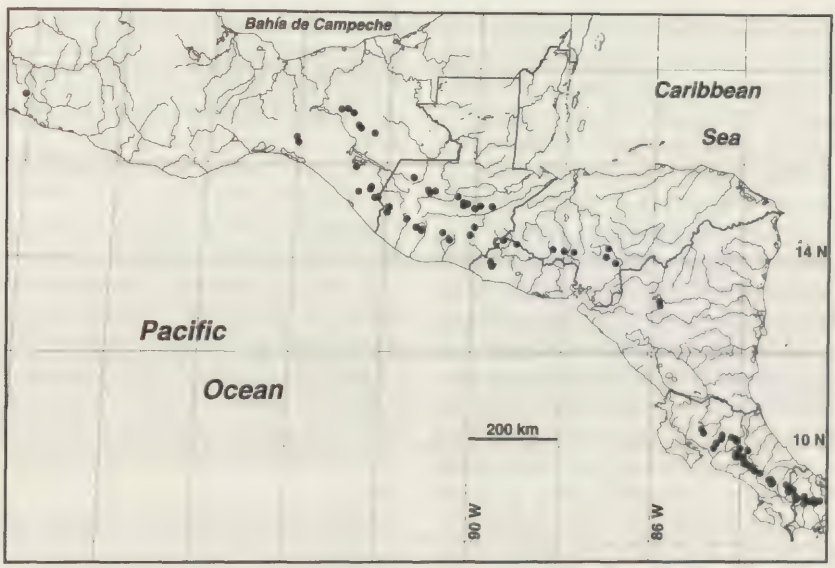


Figure 74. Distribution of *Styrax warscewiczii*.

within *Styrax* must await more detailed study of *Styrax* in South America.

18. Styrax tuxtlensis P. W. Fritsch, sp. nov. TYPE: Mexico. Veracruz: Los Tuxtlas Range, Mpio. de Mecayapan, Volcán Santa Marta, 18 May 1986, *J. V. LaFrankie 1306* (holotype, CAS; isotypes, GH, MO, TEX). Figures 25, 45, 46.

Arbor sempervirens; *lamina* lanci-ovata stellata-pubescens, basi manifeste obliqua; *inflorescentiae* ignotae; *calyx* stellatus-pubescens; *flores* ignoti; *drupa* angusta-ellipsoidea, 15–18 × 8 *mm*.

Evergreen tree to 10 m. Young twigs dark orange-brown-stellate-pubescent; outer layer of older twigs not exfoliating. Petiole 9–11 mm long. Lamina chartaceous, 7.5–10 × 3.3–3.7 cm, lance-ovate or lanceolate, secondary veins 7–10; apex gradually or abruptly short-acuminate; base distinctly oblique and slightly attenuate; adaxially glabrous except along the major veins; abaxially covered with olive-gray stellate hairs and scattered orange-brown stellate hairs, the latter particularly prevalent near and on the veins; margin entire. Inflorescence and flowers unknown. Corolla presumably valvate in bud, non-overlapping at anthesis. Infructescences axillary or false-terminal, racemose, 3–5 cm long, with about 3–6 peducles or peduncle scars. Peduncle 5–6 mm long. Fruiting calyx 2–3 mm high, shallowly cupuliform, slightly concave between the 5 minute (0.25 mm long) teeth, the exterior surface densely covered with appressed stellate or scale-like hairs, inner calyx margin glandular. Drupe 15–18 × 8 (if 1-seeded) or 12 (if 2-seeded) mm, narrow-ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Known only from the type locality on Volcán Santa Marta in the Tuxtlas range, Veracruz, Mexico; 800 m; steep volcanic slopes. Fruiting: May.

This species is known only from one fruiting collection. It can be distinguished from all other species treated here by the distinctly oblique leaf bases. *Styrax tuxtlensis* is apparently geographically isolated from all other *Styrax* species except *S. glabrescens*, from which it can be easily distinguished by its evergreen habit and drupaceous fruit. More collections of this unusual species, especially in flower, are needed to better understand its taxonomy and relationships.

19. Styrax warscewiczii Perkins, Bot. Jahrb. Syst. 31: 480. 1902. TYPE: Costa Rica or Panama. "Veragua," (1848?), *Warscewicz 203* (holotype, B destroyed; photo of holotype, GH, MICH, US; isotype, F). Figures 5, 9, 10, 71–74.

Styrax polyneurus Perkins, in Donn. Sm., Bot. Gaz. 35: 5. 1903. TYPE: Costa Rica. [San José:] "In silvis ad Copey" (protologue). Feb. 1898 (protologue: "1896"? from US specimen), *Tonduz 11744* (holotype, B destroyed; isotypes, CR, F, US).

Evergreen tree to 20(–30) m. Young twigs stellate-pubescent, the hairs usually orange-brown, sometimes yellow-brown or dark brown, rarely

greenish gray mixed with brown hairs; outer layer of older twigs not exfoliating. Petiole 5–20(–25) mm long. Lamina chartaceous, 5.2–12.5(–16.0) × 1.6–4.5(–5.4) cm, narrowly or broadly elliptic, secondary veins 9–12; apex sometimes subrounded or acute, more often cuspidate to acuminate; base cuneate or less often subrounded, symmetric or slightly oblique; adaxially glabrous except along the major veins; abaxially thickly covered with greenish white and often larger orange-brown stellate hairs, the secondary and tertiary veins glabrous to densely tomentose; margin entire. Inflorescences axillary or false-terminal, racemose or paniculate, the racemes or panicle branches 2–6 cm long, 2–21-flowered. Lower pedicels 2.5–8(–11) mm long. Calyx 2.5–4 × 3–5 mm, broadly conical or cupuliform, grayish green-radiate-lepidote, often with larger, scattered orange-brown scales especially toward the base; scales at mid-calyx 0.13–0.33 mm diam.; calyx teeth 5, to 0.5 mm long, deltoid, the calyx margin concave between the teeth, inner margin often glandular. Corolla usually pink, sometimes white, sometimes white with pink lobes, 9–17 mm long, petals connate (0–)2–6 mm beyond the calyx margin distally; corolla lobes 5, valvate in bud, 6–13 × (1–)1.5–2.5(–2.9) mm, non-overlapping, spreading or nearly erect, thickened, linear-deltoid, vesture on the outer distal third of the lobes consisting of radiate scales. Free portion of the stamen tube 1–3 mm long; distinct portion of filament (1.0–)1.3–2.5 mm long, of equal width throughout, ventrally not auriculate, white-stellate-pubescent at the somewhat incurved filament margins, glabrous or nearly so on the face proximally, increasing in pubescence distally, the hairs with radiate arms to 0.3 mm long; anthers 1.7–3.6 mm long, 1.1–2.2 times as long as the distinct portion of the filaments, the connectives not or only slightly prolonged beyond the non-tapered anther sacs. Ovary densely stellate-hirsute; style glabrous or pubescent at base only; stigma 0.3–0.4 mm wide. Drupe 7–12(–15) × 4–7(–8) mm, ellipsoid; wall irregularly and coarsely rugose on herbarium specimens. Seed coat glabrous.

Far western Panama north to western Chiapas, Mexico, disjunct to Guerrero in the Sierra Madre del Sur. One specimen collected from San Luis Potosí in the Sierra Madre Oriental, Mexico, is of uncertain status but resembles *S. warscewiczii*; most common from Chiapas to Guatemala, and in the Costa Rican cordillera; 1100–3200 m; cloud forests, *Quercus-Pinus* forests (Guerrero, Chiapas), lower montane wet forests, montane rainforests, dry montane forests, pastures, savannas; found in primary or secondary growth, in valleys and along streams, in the understory to unshaded, open situations, and roadsides, on rock outcrops, lava flows, or heavy clay loam. Flowering: apparently throughout the year; fruiting: apparently throughout the year.

Common names. Azulillo (Costa Rica, *Madriz 9*), el común (El Salvador, *Allen 6882*), estoraque (Guatemala, *Standley 58420*), estorace (Guatemala, *Steyermark 32827*), *estorach* (Guatemala, *Lamb 115*), oreja de venado (El Salvador, 4 June 1976, *Reyna s.n. p.p.*), sapuyulillo de montaña (Guatemala, *Steyermark 33315*). Standley (1938) has listed under *S. polyneurus* and *S. warscewiczii* the Costa Rican common names aguacate ascá, ascá, laurel, quiquicirrí, and resina, all of which likely apply to the concept of *S. warscewiczii* presented here.

Uses. Firewood (Guatemala, *Steyermark 33315*).

Selected specimens examined. COSTA RICA. **Alajuela:** Cinco Esquinas de Carrizal, *A. Jiménez 3653* (CR, F, MO). **Cartago:** Guarco, *Madriz 9* (CR, F, NY); near El Cañón, 40 km S of Cartago, *Williams et al. 28194* (F, NY, US). **Guanacaste:** Las Nubes, *Valerio 1396* (F). **Heredia:** S slope of Volcán Barba, *Hatheway 1258* (CR, DS, DUKE, F, GH, US). **Limón:** Valle de Silencio, *Davidse et al. 28606* (CAS, CR, DUKE, MO, NY). **Puntarenas:** Cantón de Buenos Aires, Ujarrás, El Carmen, Cerro Betsú, *I. Chacón 494* (CR, F, MO); Sitio Cotón (Cotonsito), along the road to Sitio Coto Brus, *Davidse 24632* (CR, MO). **San José:** overlooking the village of Boquete and about 20 km N of San Isidro del General, *Wilbur 21135* (AAU, BR, CAS, CR, DUKE, F, LL, MICH, MO, NY, TEX, US). EL SALVADOR. **Chalatenango:** Los Esesmiles, E of La Palma, *Allen & van Severen 7314* (F, GH, LL, NY, US). **Santa Ana:** Cerro Verde, *Allen 6853* (F, US); northern slopes of Volcán Santa Ana, *Allen 6882* (F, US); Cerro Montecristo, 4 June 1976, *Reyna s.n. p.p.* (CR). GUATEMALA. **Alta Verapaz:** Río Frío, entre Tactic y Santa Cruz, *Molina & Molina 12236* (F, NY, US). **Baja Verapaz:** Sierra de las Minas E of Chilascó, *Lamb 115* (F); Niño Perdido, *Lundell & Contreras 20452* (CAS, LL, MEXU, MO, NY). **El Progreso:** hills between Finca Piamonte, *Steyermark 43410* (F). **Escuintla:** forest vicinity of Volcán Pacaya, *Molina & Molina 27644* (F, MICH, U). **Guatemala:** upper slopes of Volcán Pacaya, *Harmon 4160* (MO, NY); Volcán de Pacaya, above Las Calderas, *Standley 58420* (A, F). **Huehuetenango:** trail between Ixteapoc and Soloma, *Steyermark 48441* (A, F). **Jalapa:** Volcán Jumay, N of Jalapa, *Steyermark 32340* (F, US); Monatañia Miramundo between Miramundo and Buena Vista, *Steyermark 32827* (A, F). **Quezaltenango:** Quebrada San Gerónimo, Finca Pirineos, *Steyermark 33315* (F). **Quiché:** Nebaj, ca. 6 km SW.W, *Contreras 5102* (DS, F, LL, US). **Sacatepéquez:** hills of Finca Carmona, SE of Antigua, *Standley 63714* (A, F, NY). **San Marcos:** Volcán Tajumulco, SW of Tajumulco, *Steyermark 36712* (F). **Sololá:** Volcán Atitlán, *Steyermark 47397* (A, F). **Suchitepéquez:** Volcán Santa Clara, between Finca El Naranjo and upper slopes, *Steyermark 46759* (A, F). **Zacapa:** upper reaches of Río Sitio Nuevo, *Steyermark 43199* (F). HONDURAS. **El Paraíso:** Mt. Yuscarán, *Molina 627* (F). **Intibuca:** Cerca de Yashse, *Molina 6522* (F, GH, US). **La Paz:** Pinares del

Huis, *Molina 6460* (F, US). **Morazán:** San Juancito, *Williams & Molina 13318* (F, GH, MO, US). **Olancho:** trail between La Chorrera campsite and 1900 m camp on ridge, *Thomas et al. 474* (MO). MEXICO. **Chiapas:** Mpio. de Motozintla de Mendoza, 45–50 km NE of Huixtla along road to Motozintla, *Breedlove & Thorne 30989* (DS, DUKE, F, MEXU, MICH, NY); Barranca Honda near Siltepec, *Matuda 4135* (A, DS, LL, MEXU, MICH, NY, US). **Guerrero:** Piedra Ancha, Puerto Hondo, *Hinton et al. 14742* (F, GH, LL, MO, NY, RSA, US, W). **Oaxaca:** Dto. de Cuicatlán, La Loma Cuyamecalco, *Conzatti 3465* (US). **San Luis Potosí:** Río de las Gallinas, Rascon, *Purpus 5317* (CAS, F, GH, MO, NY, US). NICARAGUA. **Jinotega:** along Hwy. 3, ca. 1 km NW of La Fundadora entrance, *Miller & Stevens 1402* (DUKE, MEXU, MO, NY). **Matagalpa:** Cerro El Picacho above Hotel Santa María de Ostuma, *Nee 27636* (DUKE, LL, MO, NY). PANAMA. **Bocas del Toro:** Valle de Silencio, *Antonio 1640* (MO). **Chiriquí:** along road to Bambito, *Allen 4851* (BR, F, GH, MICH, MO, NY, U, US).

Styrax warscewiczii is a widespread, relatively high-elevation species, occurring from Guerrero, Mexico, to northern Panama. A collection of *Styrax* from San Luis Potosí may be this species as well (see below). In Mesoamerica, it is the species that generally replaces the equally common *S. argenteus* above 2000 m. It is most common in Chiapas and Central America; in Mexico west of Chiapas *S. warscewiczii* has been collected only once, in the Sierra Madre del Sur, Guerrero.

Gonsoulin (1974) placed this species in synonymy under *S. argenteus* var. *ramirezii*. His annotations of specimens referred to here as *S. warscewiczii* are usually *S. argenteus* var. *ramirezii*, but five are annotated as *S. argenteus* var. *argenteus*, and six as "intermediates" of varieties *argenteus* or *ramirezii*. *Styrax warscewiczii* is easily distinguished from *S. argenteus* as circumscribed in the present revision by the lack of both auricles and stiff, long-armed, upward-pointing hairs on the stamen filaments ventrally, as well as by the presence of radiate scales rather than stellate hairs on the calyx.

Styrax warscewiczii and *S. ramirezii* are morphologically similar in many respects. Nonetheless, they exhibit enough differences throughout their ranges to justify the recognition of these two entities as species, although they are likely to be closest relatives. They can be diagnostically differentiated from each other by vesture on the outer distal third of the corolla lobes, which consists of stellate hairs in *S. ramirezii* and radiate scales in *S. warscewiczii*. The two species can be further distinguished by the other characters in couplet 18 of the key: the anthers are longer and the ratio of anther length to the length of the distinct portion of the filaments is higher in *S. ramirezii*. Besides the characters listed in the key, *S. warscewiczii* differs from *S. ramirezii* by a tendency toward smaller leaves, smaller flowers, and shorter leaf internodes. However, these characters exhibit some degree of overlap.

The two species are most similar in Oaxaca and Chiapas, where the range of the large-scaled form of *S. ramirezii* overlaps the range of *S. warscewiczii*. There are a number of morphological patterns exhibited by *S. warscewiczii* and *S. ramirezii* that suggest bidirectional introgression between the two species in this region. First, the sizes of the calyx scales are equivalent in *S. warscewiczii* and the large-scaled form of *S. ramirezii*, whereas in the other forms of *S. ramirezii* the calyx pubescence consists of smaller scales or stellate hairs. Second, the large-scaled form of *S. ramirezii* exhibits a tendency toward the anther length and anther-filament ratio typical of *S. warscewiczii*, whereas in the other two forms of *S. ramirezii* these two characters clearly distinguish the species. Third, north of Honduras and especially in Chiapas many individuals of *S. warscewiczii* possess larger leaves and longer leaf internodes than is typical for the species, and thus the measurements of these characters approach or overlap those typical for *S. ramirezii*.

If these two species are in fact closest relatives, it may be difficult to ascertain whether the patterns of morphological variation displayed in the zone of sympatry are a result of primary speciation or secondary contact. A phylogenetic estimate that resolves the sister-group status of these species would make the pursuit of this issue practical. Further investigation of this problem should focus on the area of geographic overlap, especially where the two species apparently grow together in the area west of San Cristóbal de Las Casas in Chiapas.

Several other characters are variable across the range of *S. warscewiczii*. The southernmost populations (Costa Rica, Panama) tend to possess a higher percentage of brown versus grayish green radiate scales than those farther north. In Panama the radiate scales have somewhat longer arms (e.g., *Schmalzel 1608*). Character variation in some collections of *S. warscewiczii* (i.e., *Haber 357, Haber 2917, Haber 5541*) in extreme northern Puntarenas Province, Costa Rica (Monteverde and San Luis), suggests hybridization with *S. argenteus*. These collections have a mixture of grayish green radiate scales and nearly stellate hairs on the calyx. They were found at relatively low elevation and may grow with typical *S. argenteus*, which is known from the general area where these collections were made. The flowers do not deviate from the range of variation within *S. warscewiczii* as defined here. Additional study of individuals in this area is needed to establish whether these collections are hybrids or an unusual form of *S. warscewiczii*.

Two specimens from San José Province, Costa Rica (San Gerardo de Dota), here assigned to *S. warscewiczii*, have nearly glabrous abaxial leaf surfaces (*Kappelle MK118* and *MK1530*). These are the only specimens of this species that show this type of variation. The specimens are sterile. It is possible that they are hybrids between *S. warscewiczii* and *S. glabrescens*, the latter of which grows in the same area (cf. *Kappelle MK23*), but this is unlikely given the relatively great evolutionary distance between the two species. It is also possible that they represent an undescribed taxon.

A single collection of *Styrax* belonging to the neotropical evergreen group has been made in the state of San Luis Potosí, Mexico (*Purpus 5317*). Brandegee referred this collection to *S. polyneurus* (= *S. warscewiczii*); Standley (1924) thought that it might represent an undescribed species. The leaves of this collection are narrowly elliptic with the apex broadly acute or obtuse, and the leaf internodes are unusually short. In these respects it matches no other *Styrax* collection precisely. It is not a variant of *S. lanceolatus*, which occurs both north and south of the locality at which Purpus made his collection, because that species has a stellate-pubescent calyx and distinctive lanceolate leaves. The Purpus collection resembles *S. warscewiczii* in its large radiate scales on the calyx and small leaves (relative to *S. ramirezii*), so I have tentatively placed it in *S. warscewiczii*. However, the fact that this collection is so far removed geographically from any other collection of *S. warscewiczii* makes this placement uncertain. Until more material is available from the area, especially in flower, it will remain unclear whether *Purpus 5317* represents (1) an unusual form of *S. warscewiczii*, (2) a distinct infraspecific taxon of *S. warscewiczii*, (3) an intermediate between *S. warscewiczii* and *S. ramirezii*, or (4) a new species.

Excluded Names

Styrax diplotrichus Diels, Notizbl. Bot. Gart. Berlin-Dahlem 13: 508. 1937. TYPE: Mexico. Guerrero: Sierra Madre del Sur, Gipfel des Telpitzahua, *Jena 458* (holotype, B destroyed).

I have located no authentic material referable to this name. If the collection cited by Diels does not actually represent a new species, then on a geographical basis it could be a specimen of either *S. austromexicanus* or *S. ramirezii*. The description indicates that the leaves of the specimen are 7–9 cm wide, thus excluding *S. austromexicanus* from consideration. The description, although quite general, is not inconsistent with the characters of *S. ramirezii*. However, there is sufficient uncertainty to preclude the placement of this name in synonymy.

Styrax limoncillo (Humb. & Bonpl.) Miers, J. Linn. Soc., Bot. 17: 292. 1880. = *Symplocos limoncillo* Humb. & Bonpl.

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Numerical List of *Styrax* Species

1. *S. argenteus* C. Presl
2. *S. austromexicanus* P. W. Fritsch
3. *S. conterminus* Donn. Sm.
4. *S. gentryi* P. W. Fritsch
5. *S. glabratus* Schott
6. *S. glabrescens* Benth.
7. *S. incarnatus* P. W. Fritsch
8. *S. jaliscanus* S. Watson
9. *S. lanceolatus* P. W. Fritsch
10. *S. magnus* Lundell

11a. *S. nicaraguensis* P. W. Fritsch subsp. *nicaraguensis*

11b. *S. nicaraguensis* subsp. *ellipsoidalis* P. W. Fritsch

12. *S. panamensis* Standl.
13. *S. peruvianus* Zahlbr.

14a. *S. platanifolius* Engelm. ex Torr. subsp. *platanifolius*

14b. *S. platanifolius* subsp. *mollis* P. W. Fritsch

14c. *S. platanifolius* subsp. *stellatus* (Cory) P. W. Fritsch

14d. *S. platanifolius* subsp. *texanus* (Cory) P. W. Fritsch

14e. *S. platanifolius* subsp. *youngiae* (Cory) P. W. Fritsch

15. *S. radians* P. W. Fritsch
16. *S. ramirezii* Greenm.
17. *S. steyermarkii* P. W. Fritsch
18. *S. tuxtlensis* P. W. Fritsch
19. *S. warscewiczii* Perkins

Index to Exsiccatae. Specimens are listed alphabetically by collector. Numbers in parentheses correspond to those in the numerical list of species. If more than one person participated in the collecting, only the first collector listed on the label is cited. Bracketed numbers are taken from the literature and presumed to belong to collections without number or, when following numbers in parentheses (i.e., Matuda and Sharp collections) indicate duplicates of collections where transcription errors apparently occurred.

Abbott, R. Q. 113 (16); 223 (16). Aguilar, J. I. 186 (1); 214 (1); 456 (1); 758 (1); 1335 (19). Aguilar, R. 1126 (6); 1159 (19). Aguirre B., C. 100–51 (15). Alexander, E. J. 1214 (10). Allen, P. H. 4851 (19); 6853 (19); 6882 (19); 7184 (3); 7314 (19). Almeda, F. 2400 (19); 3044 (19); 3291 (19); 3761 (19); 5642 (6). Anderson, W. R. 6109 (15). Andrie 513 (6). Antonio, T. 1640 (19). Aranda, M.

40 (1). Araquistain, M. 3635 (19). Arriaga, R. 176 (6). Arsene, B. G. 2841 (16); 5366 (16); 8472 (16). Atwood, J. A316 (11a). Avendaño R., S. 238 (6); 258 (6); 331 (6); 353 (6); 793 (6). Avila, A. de 742 (2). Ayala, M. G. 678 (15); Azofeifa, A. 6 (6).

Báez, C. G. 124 (6). Barkley, F. A. 7440 (16). Bartholomew, B. 2914 (16). Bauml, J. 531 (1). Bello, E. 932 (11a); 1031 (6); 2158 (6); 2944 (6); 5310 (6). Berlandier, J. 429 (6). Boege, W. 1765 (16). Bossé, G. 8222 (1); 8335 (19). Botteri 1006 (16). Boutin, F. 2878 (4). Boyle, B. 3841 (16). Brave 2015 (19). Breedlove, D. E. 6366 (1); 6439 (1); 7619 (1); 8917 (6); 10188 (6); 14085 (1); 15588 (4); 16893 (4); 18269 (4); 18414 (4); 18584 (4); 20577 (1); 20635 (1); 21827 (19); 21943 (1); 22841 (19); 23352 (1); 24991 (6); 25152 (1); 25292 (19); 27646 (19); 28186 (6); 28487 (1); 29307 (1); 29696 (1); 30187 (6); 30255 (1); 30989 (19); 31045 (10); 31106 (10); 31368 (19); 32394 (10); 32773 (1); 33804 (1); 34377 (6); 39600 (10); 39966 (1); 40224 (19); 40415 (6); 41339 (19); 41446 (10); 41611 (19); 42421 (1); 45097 (8); 45657 (16); 46223 (10); 46979 (1); 48026 (1); 49750 (10); 50020 (19); 50206 (1); 50712 (1); 51000 (1); 52664 (6); 52994 (19); 55749 (19); 57053 (10); 58137 (6); 59921 (16); 61642 (8); 61786 (16); 64233 (16); 64437 (16); 64929 (2); 64955 (16); 65176 (2); 67582 (6); 68742 (10); 68828 (6); 68928 (3); 69019 (6); 69083 (19). Brenes, A. M. 180 (6); 298 (6); 345 [258] (1); 3683 (1); 3772 (19); 3971 (19); 3986 (6); 4462 (19); 5403 (19); 5506 (19); 6079 (6); 6380 (19); 6410 (1); 6464 (1); 6734 (6); 6823 (6); 11458 (19); 13599 (6); 17008 (1). Bullock, S. H. 2024 (15). Burger, W. 7390 (19); 7707 (19); 7713 (19); 12004 (6); 12064 (19); 12153 (6); 12400 (6); 12475 (6).

Cabrera, E. 1404 (1); 1405 (1); 1988 (1); 3805 (10). Calvert, B. 53 (16). Calzada, J. I. 3076 (6); 4333 (6); 5249 (6); 5534 (6); 8791 (6); 9902 (1); 17816 (8); 17822 (8); 17840 (15); 17960 (6); 18805 (15). Campos, A. 3467 (15). Campos, P. 177 (6). Campos V., A. 3545 (1); 4740 (16). Cárdenas, A. L. 79 (15). Carlson, M. C. 690 (19); 2710 (6). Carranza, E., 4033 (9); 4465 (9); 4519 (16). Castillo C., G. 1573 (6); 2203 (6). Cedillo T., R. 670 (6); 1986 (1); 2356 (6). Cevallos, J. 72 (16). Chacón, A. 494 (19). Chacón, I. A. 1562 (19); 1577 (1). Chavarría, M. M. 631 (19). Chávez, C. 521 (19); 540 (11a). Cházaro B., M. 1196 (6); 1511 (6); 4675 (6); 5485 (8). Cházaro, M. 2685 (6); 2691 (6); 3759 (6); 6993 (8). Chinchilla, M. 183 (6). Chrysler, M. A. 5590 (19). Cochrane, T. S. 10792 (16); 11942 (15); 12047 (15); 12546 (16). Contreras, E. 4915 (19); 4924 (19); 5102 (19); 11029 (19). Conzatti, C. 2338 (16); 2450 (16); 3465 (19); 3480 (6); 4558 (1). Cooper, J. J. 10321 (19). Córdoba, J. J. 754 (1). Correll, D. S. 29152 (14a); 29572 (14a); 37003 (14a); 37024 (14a). Cory, V. L. 34763 (14c); 34765 (14c); 34937 (14d); 34938 (14d); 34939 (14d); 34940 (14d); 37767 (14d); 37769 (14d); 38763 (14d); 38764 (14d); 38933 (14d); 38934 (14d); 42659 (14d); 42661 (14d); 42664 (14d); 42666 (14d); 42668 (14d); 42669 (14d); 42673 (14d); 42677 (14d); 42678 (14d); 42953 (14d); 42956 (14d); 49179 (14d); 49453 (14c); 49454 (14c). Cowan, C. P. 4612 (19). Croat, T. B. 34830 (19); 34981 (19); 37190 (13); 45262 (15); 48197 (16); 64211 (6). Cruz C., R. 534 (16). Cuevas G., R. 709 (15); 1251 (16); 1294 (16); 1366 (16); 1876 (15); 1927 (16); 2213 (16); 2391 (15); 2423 (16); 2864 (16); 2890 (16); 4032 (16). Cufodontis, G. 461 (19).

D'Arcy, W. G. 9887 (19); 9992 (19). Darío, M. 59 (3); 72 (6); 119 (6); 142 (6). Davidse, G. 1511 (19); 1654 (19); 1656 (6); 10164 (19); 10216 (19); 24017 (19); 24409 (19); 24511 (19); 24632 (19); 26146 (19); 28381 (6); 28554 (19); 28606 (19); 28668 (19); 34298 (6). Davidson, M. E. 776 (19). Delgado S., A. 849 (19). de Nevers, G. 6018 (19); 6848 (13). De Niz L., D. 23 (15); 290 (16). Díaz B., H. 2106 (16); 2265 (16); 3656 (16); 4700 (16). Díaz Luna, C. L. 3592 (16). Dieterle, J. V. A. 4023 (15). Diggs, G. 3804 (16). Domínguez C., R. 28 (4). Dorantes, J. 574 (6). Dorr, L. J. 1910 (14a); 1918 (14d). Dryer, V. J. 1261 (6); 1420 (11a); 1575 (11a). Dwyer, J. D. 454 (1); 7006 (19).

Ebinger, J. E. 716 (19). Edwards, J. B. P–290 (1). Ehrenberg 498 (16). Emrick, G. M. 60 (16). Erazo, M. 63 (1). Escobedo, J. M. 1063 (16); 1783 (16). Espinoza, R. 128 (1); 169 (1); 234 (1); 682 (1); 1254 (19). Eugenio, J. 388 (1). Evans, R. 1726 (19).

Fairey, J. T26M–79p–101490 (9); T39M–3.5h–031992 (6). Fernández, A. 807 (6); 1444 (19). Ferrera B., A. 176 (1). Flores C., J. 315 (16). Flores F., G. 793 (16); 1907 (15); 2498 (15). Flores M., A. 2680 (16). Flores-Franco, G. 3344 (15). Folsom, J. P. 6047 (19). Fonseca J., R. M. 163 (2). Frankie, G. W. 239 (1). Fuentes O., M. 56 (16); 90 (16). Fuentes, Z. 192 (11a).

Galeotti, H. 1687 (16); 2851 (6); 2852 (6). Gamboa, B. 71 (19). García, A. R. 1902 (19). Garwood, N. 334 (19); 761 (1); 1404 (6). Gentry, A. 13797 (12?); 14073 (12?). Gentry, H. S. 4420 (4); 5164 (15); 6244 (4); 10485 (15); 10811 (15); 10863 (15). Ghiesbreght, A. B. 620 (1); 811 (19). Gilly, C. L. 64 (6). Glassman, S. F. 1956 (19). Gliessman, S. R. CH–54 (19). Gold 129 (16). Goldman, E. A. 872 (1). Gómez, L. D. 20777 (1). Gómez-Laurito, J. 8012 (6); 9681 (19); 11345 (6); 11383 (19); 11445 (6). Gómez-Pompa, A. 793 (6). Gonsoulin, G. 1287 (14a); 1288 (14a); 1289 (14a); 1305 (14a); 1306 (14a); 1307 (14a); 1308 (14a). González, J. 108 (1); 340 (16); 627 (19). González L., M. 78 (16). González Q., L. 3347 (16). González-Espinosa, M. 1148 (19); 1279 (19); 1659 (19). González-Villareal 4053 (1). Grayum, M. H. 6453 (19). Gregg, J. 955 (8). Guerrero 322 (8). Guerrero N., J. J. 649 (16). Gutiérrez, G. 124 (6). Gutiérrez, M. 239 (16). Guzmán M., R. 2516 (16).

Haber, W. 230 (11b); 357 (19); 363 (6); 404 (1); 2917 (19); 3173 (13); 3533 (1); 4330 (6); 5541 (19); 6116 (1); 7353 (6); 7526 (19); 9318 (13); 10631 (6); 11118 (19); 11381 (1). Haenke, T. s.n. and [148] (1). Hagen, C. von 1253 (1). Halbinger, C. 220 (16). Hammel, B. 5734 (19); 6729 (19); 13812 (6); 15271 (6); 19068 (19); 20076 (6). Hansen, B. 1479 (16). Harmon, W. E. 3056 (1); 3461 (1); 4160 (19). Hartshorn, G. S. 1075 (19); 1805 (1); 1894 (11b); 2119 (6). Hartweg 489 (6). Hatheway, W. H. 1258 (19). Hazlett, D. 18–22 Nov. 1974 (6); 667 (1). Heller, C. 234 (6). Helmrich, H. 1690 (6). Henrickson, J. 11499 (14e); 11561 (14e). Henry, M. G. 6557 (14a); 6560 (14c). Hernández, G., L. 322 (16). Herrera, G. 297 (1); 472 (6); 854 (1); 2046 (6); 3532 (19); 4534 (5); 4911 (6); 5866 (17); 5957 (6). Heyde, E. T. 2915 (3); 6182 (1). Hinton, G. B. 3798 (16); 5282 (16); 5309 (15); 6145 (16); 6193 (15); 7410 (15); 7605 (16); 7606 (16); 7618 (16); 7685 (16); 10400 (16); 11831 (16); 14409 (16); 14742 (19); 14750 (2). Hitchcock, C. L. 7103 (16); 7105 (16). Holdridge, L. R. 2299 (17); 2338 (6). Huerta, M., M. 233 (16).

Iltis, H. H. 337 (16); 389 (15); 459 (15); 2516 (16). I INBio 16 (13). II InBio 164 (11b).

Janzen, D. H. 12108 (1). Jardel, E. 214 (16). Jermy, G. 105 (14a). Jiménez M., A. 345 (1); 1285 (1); 1974 (19); 2305 (19); 3511 (1); 3653 (19); 3983 (19). Jiménez, O. 420 (1); Jiménez, Q. 308 (1); 699 (6); 749 (1). Jiménez, W. 99 (19). Johnson, J. C. 599 (14c). Johnston, M. C. 7304 (14d); 7408 (9); 7428 (14d); 11888 (14e); 11925 (14e); 12845 (9). Juárez, L. G. 62 (6). Judziewicz, E. J. 4792

(16); 4899 (16); 4973 (16); 5038 (16); 5098 (16); 5212 (15). Juzepczuk, S. 1598 (1).

Kappelle, M. MK23 (6); MK74 (19); MK118 (6); MK119 (19); MK407 (19); MK417 (19); MK483 (19); MK505 (6); MK861 (6); MK892 (19); MK1088 (19); MK 1176 (19); MK1535 (19); 2800 (19); 2875 (19). Keeney, T. 1456 (14d); 1457 (14d). Kellerman, W. A. 5664 (1); 6415 (1); 7642 (1). Koch, S. D. 7643 (16); 7929 (16). Kowal, R. R. 2805 (16). Kuntze, O. 2286 (19).

LaFrankie, F. V. 1306 (18). La Gaza s.n. (6). Lagos-Witte, S. 86 (19). Laguna, A. 279 (1); 351 (1). Lamb, F. B. 115 (19). Lankester, C. H. 139 (6). Lao, E. A. 349 (19); 359 (19). Laughlin, R. M. 408 (16). Lavin, M. 4591 (1). Lems, K. 5340 (19). Lent, R. W. 1681 (19); 1932 (6); 3920 (19). León, J. 269 (19); 295 (19); 3675 (19). Liebmann, M. F. 424 (6); 589 (6); 596B (16). Liesner, R. 14480 (6); 14600 (6); 15533 (6); 26612 (6). Linden, J. J. suppl. 7 (6); 76 (6); 358 (19). Little, E. L. 6043 (19); 9932 (10); 20061 (1). López, E. 7555 (1). López R., R. M. 503 (6). Lorea H., F. G. 43 (16). Lott, E. J. 2540 (15). Lundell, C. L. 12631 (6); 19214 (17); 19450 (7); 19618 (7); 20452 (19); 20933 (7); 21126 (6); 21172 (6); 21219 (17). Lyonnet, E. 2106 (16); 1341 (16).

MacDaniels, L. H. 942 (6). MacDougall, T. H155 (15); H156 (15). Machuca N., J. A. 6636 (16). Madriz V., A. 9 (19); 67 (1). Magallanes, A. S. 1534 (15); 3432 (15). Magaña, R. H. 5607 (6); 5785 (6); 6109 (6). Makrinus, E. 551 (15). Mancera O., A. MO–315 (16). Márquez, W. 141 (6); 847 (6); 882 (6). Martin, G. J. 501 (6). Martín J., S. 1208 (1). Martínez A., M. 55 (16). Martínez, J. L. 1300 (6). Martínez S., E. 327 (16); 429 (16); 2857 (16); 3908 (16); 4906 (2). Martínez-Ico, M. 160 (19). Matuda, E. 467 (19); 568 (19); 2668 (19); 2982 (10); 3930 (19); 4135 (19); 4179 (6); 4335 (6); 5102 (6); 5215 (1); 15410 [5410] (6); 15507 (3); 15922 (6); 15995 [5995] (6); 16265 (19); 17816 (6); 28364 (16); 30405 (16); 30566 (16); 30833 (16); 30858 (16); 31979 (16). Mayfield, M. H. 1632 (15). McCaffrey, D. 77 (1). McPherson, G. 9255 (19). McVaugh, R. 541 (15); 10304 (16); 11764 (16); 11766 (16); 12061 (8); 12100 (15); 13369 (8); 13914 (16); 14279 (16); 15025 (16); 21521 (16); 22813 (16); 23250 (15); 23415 (15); 23515 (15); 23593 (16); 25492 (15); 26020 (16); 26376 (15). Meave, J. 1162 (1). Medina G., C. 1750–a (16). Medrano, F. G. 2488 (6); 5032 (16); 5044 (16); 5176 (16); 5191 (16); 6201 (19); 6706 (2); 6785 (16); 6821 (16); 6833 (16); 17054 (16); 17405 (6); 17436 (6); 17455 (6). Mendoza, A. G. 3802 (16); 3862 (16). Mexía, Y. 1351 (15); 1504 (16); 1861 (15); 9059 (16). Meyer, E. 267 (16). Miller, J. S. 1402 (19); 2608 (16); 2752 (19); 3092 (16); 3114 (16); 3140 (15); 5145 (14c). Miranda, F. 161 (16); 1214 (16); 1580 (16); 3066 (16); 3460 (6); 5295 (1); 5927 (1); 7020 (6); 7055 (19); 7232 (19); 9170 (10); 9173 (6); 9199 (6). Molina R., A. 627 (19); 6460 (19); 6522 (19); 7233 (6); 7524 (1); 12236 (19); 17086 (19); 20321 (1); 21341 (1); 21505 (19); 24404 (6); 24561 (1); 25328 (1); 27644 (19); 34417 (1). Montes, M. 714 (15). Moore, H. E. 3231 (6); 6225 (6). Mora, C. E. 3, p.p. (19). Mora, G. 229 (19). Moraga, M. 263 (6). Morales, J. F. 111 (19); 4266 (6). Moran, R. 10161 (15). Moreno G., S. 38 (16); 176 (16). Moreno, P. P. 480 (19); 1883 (1); 10854 (1); 16366 (11a); 17875 (1); 21064 (1); 21279 (1); 22001 (1); 22569 (1); 23512 (1). Mori, S. 7359 (19); 7416 (19). Morones G., A. 209 (16). Motte, M. E. 37 (16). Muñoz, E. 4 (19); 36 (16). Museo Nacional 17924 (1).

Narave, H. 42 (6); 55 (6); 468 (6). Nee, M. 24719 (6); 26290 (6); 27636 (19). Nees s.n. [1885?] (1). Negrete A., M. 45 (16). Neill, D. 2313 (19). Nelson, E. E. 3750 (6); 6886 (16). Nevling, L. I. 2441 (6). Nieves H., G. 50 (8); 411 (15); 546 (15). Norris, D. H. 14959 (15). Núñez, J. C. S. 4739 (16); 4785 (16); 5243 (6); 6291 (16); 6328 (16).

Opler, P. A. 523 (1). Orozco, J. M. 329 (1). Örsted, A. S. 591 (1); 11194 (19). Ortega, J. G. 60 (15); 4118 (15); 5082 (15).

Palacios E., E. 34 (1); 1442 (1); 161 (10). Palafox R., M. 1 (6). Palmer, C. W. 97 (6). Palmer, E. J. 9843 (14c); 10237 (14c); 10907 (14a); 11474 (14c); 11528 (14c). Panero, J. 3475 (2); 5254 (2). Paray, L. 681 (6). Parks, H. B. 1009 (14c); 1942 (14c); 40988 (14c). Pérez J., L. A. 814 (15). Pérez, S. 17 Sep. 1987 (8). Peterson, C. D. 1243 (14b). Pichardo A., V. 14 (16); 28 (16); 111 (16); 212 (16). Pittier, H. 606 (1); 1583, p.p. (1); 1583, p.p. (19); 2140 or 2265 (6); 4242 (12); 5076 (1); 6583 (6). Plowman, T. 14547 (15). Poole, J. M. 1205 (14c). Poveda, L. 223 (1); 1728 (19); 1730 (6); 3843 (1). Pringle, C. G. 2978 (8); 3486 (8); 4416 (8); 6848 (16); 8023 (16); 8129 (6); 9000 (16); 11012 (8); 13104 (6). Proctor, G. R. 25210 (6); 25299 (19); 25514 (19); 31886 (19). Purpus, C. A. s.n. May 1925 "with 10057" (1); 46 (1); 82 (19); 157 (19); 1925 (6); 5317 (19); 7422 (3); 9280 (6); 10082 (19); 10088 (6); 10521 (6); 10531 (1); 10545 (6); 10555 (19); 10612 (6); 13001 (1); 14301 (1).

Quirós, M. 180 (6).

Ramírez D., R. 259 (8); 477 (15). Ramírez, M. 77 (19). Ramírez R., R. 894 (15). Ramírez-Marcial, N. 504 (6); 553 (19). Ramos, P. X. 86 (16). Reko, B. P. 3642 (15); 4136 (6). Reverchon, J. 1551 (14a). Reyes García, A. 356 (1); 463 (1). Reyes, J. R., 1640 (6). Reyna B., O. 309 (16). Riskind, D. H. 1682 (14c); 1691 (14c); 1915 (14e); 2079 (14e). Rivera, G. 198 (19); 749 (1); 1851 (6). Robles, L. 813 (15). Robleto, W. 87 (6). Rodríguez, J. V. 2004 (1); 2100 (1); 3669 (1); 3760 (1); 10194 (1). Rose, J. N. 7236 (16). Rubio, H. 1583 (6); 1711 (6). Rzedowski, J. 14553 (16); 17211 (6); 18362 (16); 18371 (16); 18529 (2); 19771 (16); 22118 (16); 30304 (16); 39745 (16).

Salazar L., S. 5 (8). Sanders, A. C. 4405 (16). Sandoval 14 (1). Santana M., F. J. 8 (16); 2695 (16); 3303 (15); 4536 (16); 4776 (15). Sartorius 92 (6). Saynes V., A. 1437 (15). Schmalzel, R. J. 1608 (19); 1756 (19). Schmitz 505 (16). Schwabe, W. 224 (1); 77566 (16). Servín, S. 15 (6); 258 (6); 1056 (6). Sessé, M. 4967 (16). Sharp, A. J. 3460 (6); 4673 (6); 4676 (6); 4677 (19); 4684 (6); 45107 [451047] (3); 45262 (19); 45382 (6); 45499 (16); 45559 (6); 45834 (6); 46154 (6); 46173 (6); 46209 (6). Skutch, A. F. 1935 (1). Smith, A. A113 (19); P1971 (19); P2623 (19); 65 (19); 176 (19); 2700 (19); 4165 (19); 4232 (19); 10079 (19). Smith, C. E. 4473 (19); 4512 (6). Smith, J. 517 (14c); 678 (14c). Smith, J. D. 2266 (1). Smith, J. F. 393 (19). Smith, L. C. 347 (16). Smith, R. F. M149 (14b). Smith, S. G. 6012 (6). Snyder, B. 274 (14c). Soejarto, D. D. 5306 (16). Solheim, S. 1397 (16). Soto Arenas, [M. A.] 1179 (16). Sousa, M. 11635 (1). Standley, P. C. 1674 (1); 1739 (1); 5007 (1); 5686 (1); 6344 (1); 8019 (19); 12351 (1); 14121 (19); 15170 (1); 15875 (1); 15947 (1); 20147 (1); 20405 (1); 32549 (19); 33500 (6); 34672 (19); 41410 (19); 42216 (19); 42254 (19); 42345 (19); 42656 (19); 51137 (6); 51175 (6); 51309 (6); 57958 (1); 58420 (19); 62879 (1); 63714 (19); 63786 (19); 64767 (1); 67865 (6); 68618 (10); 70316 (6); 77656 (1); 80536 (19); 80605 (19); 80659 (19); 80684 (19); 81378 (1); 82830 (1); 82938 (1); 83018 (1); 83697 (6); 85559 (10); 91569 (19); 91577 (19); 92302 (19); 92400 (19); 92574 (19); 92631 (19). Stern, W. L. 1993 (19); 2045 (19). Stevens, W. D. 86 (19); 6687 (6); 13694 (19); 15494 (1); 20401 (11a); 22180 (19);

22709 (1). Steyermark, J. A. 30624 (1); 30672 (1); 30728 (1); 31150 (1); 32340 (19); 32827 (19); 33138 (1); 33315 (19); 33926 (19); 35418 (1); 36234 (10); 36712 (19); 36801 (10); 36807 (6); 37378 (6); 37989 (19); 42075 (1); 42742 (1); 43199 (19); 43279 (3); 43410 (19); 43593 (19); 43937 (19); 46750 (6); 46759 (19); 47397 (19); 47924 (1); 48441 (19); 48666 (17); 48848 (17); 49738 (6); 49982 (3); 50429 (1); 50699 (1); 50776 (1); 50801 (1); 51100 (1). Stone, D. E. 3286 (6). Sullivan, J. R. 543 (6).

Tapia, L. 80 (6). Taylor, C. M. 3210 (19). Taylor, J. 2956 (6); 11848 (19); 17390 (1). Téllez V., O. 10139 (16); 10282 (15); 10412 (15). Templeton, B. C. 7000 (15). Tenorio L., P. 2642 (2); 8364 (15); 8441 (15); 14351 (16); 15605 (15); 16929 (15); 16984 (15). Tenorio, P. 5707 (1). Terry, M. E. 1338 (19); 1348 (19). Thomas, H. 26 (7); 474 (19); 496 (6). Ton, A. S. 404 (1); 3431 (1); 6494 (1); 7814 (6); 7963 (10); 9329 (16); 9734 (10). Tonduz, A. 459 (19); 7079 (1); 7447 (1); 7667 (6); 9816 (1); 11744 (19); 17924 (1). Toriz A., G. 464 (6); 475 (6). Torres C., R. 2686 (6); 4982 (6). Torres, R. 13321 (16). Tróchez, L. 17 (1). Tyson, E. L. 826 (19); 827 (19).

Ugent, D. 1635 (16). Umaña, G. 71 (19); 144 (19). Utley, J. 4557 (19).

Valdez, G. L. 616 (2). Valerio, Man. 1378 (1); 1396 (19). Valerio, Mar. 145 (19); 174 (19). Vásquez S., J. 2174 (16). Vázquez, A. 1195 (15); 4164 (15); 4625 (6). Vázquez M., A. 4529 (16). Vela G., L. 2050 (16). Velázquez H., A. 13 (8). Velzen, H. van 2765 (19). Ventura A., F. 784 (6); 866 (6); 1195 (6); 3408 (6); 3511 (6); 5211 (6); 8071 (6); 8116 (6); 12945 (6); 20283 (6); 20303 (6). Vergas, C. 285 (6). Villarreal, L. M. 4585 (8). Villaseñor, J. L. 183 (16). Vincelli, P. C. 424 (19). Voorhies, B. 3–11 (1); 5–3 (1); 16–9 (1).

Walker, S. 72.021 (16); 73H07 (15). Warscewicz, J. 40 (1); 203 (19). Wawra 1011 (6). Weaver, R. E. 1745 (6); 1754 (6). Webster, G. L. 12230 (19); 12496 (11a). Wendt, T. 148b (14e); 582 (14e); 3576 (12?). Werff, H. van der 6301 (19). Wetter, M. A. 2007 (16); 2057 (16). White, G. 70 (19). White, S. S. 5260 (1). Wiemann, M. C. 32 (19). Wilbur, R. L. 1766 (16); 8821 (19); 16166 (19); 16223 (19); 18026 (1); 21135 (19); 22584 (19); 23494 (19); 27228 (19); 29475 (19). Williams, L. O. 10491 (1); 11279 (1); 12136 (1); 12314 (1); 12648 (19); 12709 (1); 13270 (1); 13318 (19); 13581 (19); 13709 (19); 14028 (1); 16067 (1); 16131 (19); 16260 (19); 17455 (19); 20001 (19); 23955 (11a); 24844 (19); 25087 (1); 28194 (19). Woodson, R. E. 484 (19); 919 (19). Woronow, G. 99b (16). Wynd, F. L. 340 (14b).

Yuncker, T. G. 5589 (1); 6175 (6).

Zamora V., N. 1213 (6). Zavala C., F. 295 (6). Zola B., M. G. 526 (6); 612 (6). Zúñiga, R. 169 (6); 575 (6); 607 (1).

Appendix 1. Comparison of Gonsoulin's (1974) treatment of *Styrax* from western Texas, Mexico, and Mesoamerica to the present revision. Synonyms are indented. Specimens of the seven taxa at the end of the right column were not available at the time of Gonsoulin's revision. (D) = deciduous.

Gonsoulin, 1974	Present revision
S. argenteus var. argenteus	S. argenteus
S. panamensis	S. panamensis
	S. radians, *sp. nov.*
	S. austromexicanus, *nom. et stat. nov.*
S. argenteus var. hintonii	S. ramirezii
S. magnus	S. magnus
S. argenteus var. ramirezii	S. ramirezii
S. orizabensis	S. ramirezii
S. warscewiczii	S. warscewiczii
	S. steyermarkii, *sp. nov.*
S. conterminus	S. conterminus
S. glabrescens var. glabrescens (D)	S. glabrescens (D)
S. glabrescens var. pilosus (D)	S. glabrescens var. pilosus
S. jaliscanus (D)	S. jaliscanus (D)
	S. gentryi, *sp. nov.*
S. platanifolius var. platanifolius (D)	S. platanifolius subsp. platanifolius (D)
S. platanifolius var. stellatus (D)	S. platanifolius subsp. stellatus, *comb. et stat. nov.* (D)
S. texanus (D)	S. platanifolius subsp. texanus, *comb. et stat. nov.* (D)
S. youngiae (D)	S. platanifolius subsp. youngiae, *comb. et stat. nov.* (D)
	S. platanifolius subsp. mollis, *subsp. nov.* (D)
	S. glabratus
	S. lanceolatus, *nom. et stat. nov.*
	S. incarnatus, *sp. nov.*
	S. nicaraguensis subsp. nicaraguensis, *sp. nov.*
	S. nicaraguensis subsp. ellipsoidalis, *subsp. nov.*
	S. peruvianus
	S. tuxtlensis, *sp. nov.*
Total: 7 species, 11 taxa	Total: 19 species, 24 taxa

Appendix 2. Index to scientific names in taxonomic part. Numbers in parentheses correspond to taxon numbers in the text. Synonyms and excluded names are italicized.

Adnaria Raf. 712
Benzoin Hayne 712
Cyrta Lour. 711
Darlingtonia Torr. 712
Epigenia Vell. 712
  integerrima Vell. (5) 725
Foveolaria Ruiz & Pav. 712
Styrax L. 711
  argenteus C. Presl (1) 714
    var. *grandiflorus* E. Carranza (2) 718
    var. *hintonii* (Bullock) Gonsoulin (16) 747
    var. *micranthus* (Perkins) D'Arcy (16) 747
    var. *parvifolius* E. Carranza (9) 733
    var. *ramirezii* (Greenm.) Gonsoulin (16) 747
  austromexicanus P. W. Fritsch (2) 718
  conterminus Donn. Sm. (3) 720
  cyathocalyx Perkins (16) 747
  diplotrichus Diels 756
  erymophyllus Pohl (5) 725
  gentryi P. W. Fritsch (4) 723
  glabratus Schott (5) 725
  glabrescens Benth. (6) 725
    var. *pilosus* Perkins (6) 727
  guatemalensis Donn. Sm. (6) 727
  hintonii Bullock (16) 747
  incarnatus P. W. Fritsch (7) 730
  jaliscanus S. Watson (8) 731
  lanceolatus P. W. Fritsch (9) 733
  lauraceus Perkins (5) 725
  leiophyllus Miers (5) 725
  limoncillo (Humb. & Bonpl.) Miers 756
  magnus Lundell (10) 734
  micranthus Perkins (16) 747
  myristicifolius Perkins (1) 714
  nicaraguensis P. W. Fritsch (11) 736
    subsp. ellipsoidalis P. W. Fritsch (11b) 737
  officinalis var. *jaliscanus* (S. Watson) Perkins (8) 731
  orizabensis Perkins (16) 747
  panamensis Standl. (12) 738
  peruvianus Zahlbr. (13) 738
  pilosus (Perkins) Standl. (6) 727
  platanifolius Engelm. ex Torr. (14) 739
    subsp. mollis P. W. Fritsch (14b) 742
    subsp. stellatus (Cory) P. W. Fritsch (14c) 743
    subsp. texanus (Cory) P. W. Fritsch (14d) 744
    subsp. youngiae (Cory) P. W. Fritsch (14e) 744
    var. *stellatus* Cory (14c) 743
  polyanthus Perkins (1) 714
  polyneurus Perkins (19) 753
  psilophyllus A. DC. (5) 725
  radians P. W. Fritsch (15) 745
  ramirezii Greenm. (16) 747
    var. *micranthus* (Perkins) Perkins (16) 747
    var. *orizabensis* (Perkins) Perkins (16) 747
  squamulosus M. F. Silva (5) 726
  steyermarkii P. W. Fritsch (17) 751
  texanus Cory (14d) 744
  tuxtlensis P. W. Fritsch (18) 753
  vestitus Lundell (6) 727
  vulcanicola Standl. & Steyerm. (10) 734
  warscewiczii Perkins (19) 753
  youngiae Cory (14e) 744
Strigilia Cav. 711
  argentea (C. Presl) Miers (1) 714
  glabrata (Schott) Miers (5) 725
  leiophylla (Miers) Miers (5) 725
  psilophylla (A. DC.) Miers (5) 725
Tremanthus Pers. 711

SYSTEMATICS OF *KALIMERIS* (ASTERACEAE: ASTEREAE)[1]

Hong-ya Gu[2] *and Peter C. Hoch*[3]

Abstract

The genus *Kalimeris* (Asteraceae: Astereae) comprises a monophyletic group, with the exclusion of section *Cordifolium*, characterized by laterally compressed achenes with short pappus bristles no longer than the length of the corolla tube. This genus of herbaceous perennials is native in East Asia and generally occurs in disturbed habitats. It has close relationships with Asian *Aster* and *Heteropappus*, as revealed by external as well as internal morphological comparisons and cytological studies. Its supposed relationship with the North American genus *Boltonia* is shown to be superficial. The species of *Kalimeris* are all closely related, and comprise a polyploid series ranging from diploid to 12-ploid with $x = 9$. Eight species and ten subspecies of *Kalimeris* are recognized in this treatment.

Kalimeris (Asteraceae: Astereae) is native in East Asia, ranging from the Amur basin in northeastern Asia at 50°N through China, Korea, and Japan to northern Indochina at 16°N, and westward to northern Myanmar (Burma) at 97°E. Most species occur in China. Although it is segregated from *Aster* by most Asian botanists, its taxonomic status as well as its delimitation have been controversial. In order to clarify the taxonomic status of *Kalimeris* and its phylogenetic relationships within Astereae, to establish its infrageneric delimitation and phylogeny, and to improve our understanding of the biosystematically poorly known Asian Astereae, we undertook studies on the morphology, cytology, and geography of *Kalimeris* and some related genera. The results of the cytological study and an RFLP analysis on rDNA of some *Kalimeris* species were published in separate papers (Gu, 1989; Gu & Tara, 1990; Gu et al., 1994). The present treatment was based on results of those surveys, in which we treat *Kalimeris* (excluding sect. *Cordifolium*) as a monophyletic taxon of eight species, distinct from *Aster* and other Asian Astereae.

Taxonomic History of *Kalimeris*

The name *Kalimeris* was first published as a subgenus of *Aster* by Cassini in 1822 (see Cassini in King & Dawson, 1975). The only species he described in that subgenus was based on a single cultivated plant that he illegitimately named *Kalimeris platycephala*. In 1825, he elevated the subgenus to generic level based on its distinctive short pappus bristles, conical receptacles, and flat achenes.

Shortly thereafter, Blume (1826) published a monotypic genus, *Asteromoea*, into which he transferred *Aster indicus* L. Subsequent treatments of Astereae by other botanists have differed substantially in the delimitation of *Kalimeris* and *Asteromoea*.

Nees (1832) expanded Cassini's concept of *Kalimeris* by transferring into it four species of *Aster* with longer pappus bristles; these were treated in the genus *Heteropappus* in most subsequent treatments by other botanists. Nees maintained *Asteromoea* as a distinct monotypic genus. He altered *Kalimeris* to *Calimeris*, a spelling that has been

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[2] College of Life Sciences, Peking University, Beijing, 100871, People's Republic of China.

[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.

taken up by several botanists since then. DeCandolle (1836) adopted Nees's system and transferred two more species of *Aster* into *Kalimeris*. Hoffmann (1890) also recognized *Asteromoea* as a separate genus, but treated *Kalimeris* sensu Nees as a section of *Aster* (sect. *Calimeris*), a treatment also followed by Nakai (1911, 1919) and Grau (1977). Part of the reason for the consistent separation of *Kalimeris* from *Asteromoea* is that the inclusion of the species with long pappus bristles in *Kalimeris* by Nees obscured Cassini's original concept of the genus, making the single species of *Asteromoea* with very short pappus bristles seem more distinctive than it really is. Most Asian botanists consider the types of *Kalimeris* and *Asteromoea* to be congeneric, and because *Kalimeris* has priority, it has been adopted in the present treatment.

The small North American genus *Boltonia*, described by L'Héritier (L'Héritier & de Brutelle, 1788), shares several floral and achene characters with *Kalimeris*. This led Bentham (1861, 1873) to combine the two genera with the southern North American *Dichaetophora* A. Gray to form a single genus, *Boltonia*, and to designate each of the three as a separate section. *Dichaetophora* is now generally recognized as a separate monotypic genus (Shinners, 1946; Turner et al., 1961; Grau, 1977), whereas the statuses of *Boltonia* and *Kalimeris* have continued to be controversial. Debeaux (1877) accepted Bentham's classification and described a new species, *Boltonia lautureana*, collected in China. Tamamshjan (1959) recognized this species as the only Asian *Boltonia* and retained *Kalimeris* as a separate genus. Only a few subsequent non-Asian botanists have followed either Hoffmann's (Grau, 1977) or Bentham's (Grierson, 1964) treatments, and only limited discussion on this subject is available in the literature (Grierson, 1964; Lauener, 1976; Koyama, 1983; Ito & Soejima, 1995).

Even among authors who recognize *Kalimeris* as a distinct genus, there is considerable disagreement about its delimitation and the number of taxa that should be recognized. There is no recent treatment that covers *Kalimeris* throughout its entire distributional range, although several local taxonomic treatments are available. In *The Compositae of China*, Hu (1967) transferred 4 species of *Aster* into *Kalimeris*, treating a total of 11 species in the genus in China. By contrast, in the most recent treatment in *Flora Reipublicae Popularis Sinicae* (Ling et al., 1985), 7 species were recognized. Kitamura (1937b, 1957) recognized 6 species in *Kalimeris* in his taxonomic treatment of Japanese Asteraceae and a subsequent series of articles. However, in the original *Flora of Japan*, Ohwi (1965) recognized only 4 species. Kitamura (1937b) also established 2 sections: sect. *Kalimeris* and sect. *Cordifolium*, which have been adopted by some other authors (Ohwi, 1965; Ling et al., 1985). In *Plantae Sinenses*, Handel-Mazzetti (1937–1938) used the generic name *Asteromoea* and included 7 Chinese species in it. Hu (1967) did a bibliographic study on the genera and species of Asteraceae in China, and transferred 3 more species from *Aster* into *Kalimeris* to make a total of 11. Some taxa of *Kalimeris* sensu Handel-Mazzetti and Hu were subsequently segregated into *Miyamayomena* (Kitamura, 1937b, 1982).

In the treatment of *Aster* in the new *Flora of Japan*, Ito and Soejima (1995) treated *Kalimeris* as *Aster* sect. *Asteromoea* Makino, arguing that "recent cladistical and molecular analyses reveal these species [*Kalimeris*, *Heteropappus*, and *Miyamayomena*] to be closely related to species of *Aster* s. str.," also noting that "further phylogenetic studies are needed to reconstruct a complete system in *Aster*" (Ito & Soejima, 1995).

Taxonomic Delimitation of *Kalimeris*

Generic delimitation in Astereae has long been a source of disagreement among botanists. The ways in which they treat the large and diverse genus *Aster* usually reflect their philosophy on generic concepts, and although there are many variations, in general there are two schools of thought. The first approach maintains a very inclusive generic concept of *Aster*, with subdivision of the genus into several subgenera (Bentham, 1873; Hoffmann, 1890; Grau, 1977; Jones & Young, 1983). The second approach is to segregate many distinctive small genera from *Aster*, thus adopting a narrow generic concept (see Cassini in King & Dawson, 1975; Nees, 1832; DeCandolle, 1836; Tamamshjan, 1959; Semple & Brouillet, 1980; Ling et al., 1985).

A number of small genera endemic to Asia have been segregated out of *Aster*, including *Heteropappus*, *Kalimeris*, *Galatella*, and *Turczaninowia*. An extreme case is the treatment of Astereae in the *Flora of URSS* by Tamamshjan (1959), who adopted a very narrow generic concept of *Aster*, segregating two new genera (*Kemulariella* and *Conyzanthus*), and accepting many small genera established by Cassini, Nees, and Novopokrovski. Kitamura (1937b) segregated another small genus, *Gymnaster* (later changed to *Miyamayomena* [Kitamura, 1982]), in his major treatment of Japanese Asteraceae. In order to evaluate the status of *Kalimeris*, a survey was made of 14 morphological characters

Table 1. Character comparison among several genera of Astereae.

Taxa (no. of sp.)*	Habit	Ray florets			Disk florets L(floret)/ L(lobe)	Involucre	
		Fert.	L (mm)	L/W		Shape	Series
Aster sensu str. (ca. 200)	annual perennial subshrub	+	5.5–24	4.3–10	2.1–5.2	turbinate campanulate hemispheric	2–4–8 subequal imbricate
Heteropappus (12)	biennial	+	9.6–19.6	3.6–5.5 (8)	2.5–3.9 (long) 4–8.8 (short)	hemispheric	2–3 subequal
Kalimeris (8)	perennial	+	7–22	3.9–9.4	2.2–3 (long) 3–5.1 (short)	campanulate hemispheric	3–4 imbricate
*Aster miquelianus***	perennial	+	8.7–11.2	5–7	1.7–3	hemispheric	2–3 subequal
Boltonia (4)***	perennial	+	4.7–13	6.3–8.1	3.6–6	campanulate	3–4 imbricate
Miyamayomena (5)****	perennial	+	8–19.5	4.1–7.3	1.7–3.7	turbinate campanulate hemispheric	2–1 subequal imbricate
Asterothamnus (4)	subshrub	+	8.5–10	4–6.4	4.5–5	turbinate hemispheric	3–4 imbricate
Galatella (22)	perennial with woody base	−	11.5–22	4.7–7.7	1.9–3.4	turbinate campanulate hemispheric	3–4 imbricate
Linosyris (3)	subshrub	X	X	X	3.2–9.7	turbinate	several imbricate

Abbreviations: A: pappus as long as the disc corolla; B: pappus ½ as long as the disc corolla; C: pappus ¼–⅕ as long as the disc corolla; D: two awnlike and fragile bristles; E: pappus two or more series, and longer than the disc corolla; fert.: fertile; L: length; long: longer lobe; short: shorter lobes; W: width; X: absent; +: yes; −: no; ±: more or less.

* Unless noted otherwise, the number of species is based on Kitamura (1937b), Jones (1980), Ling et al. (1985), and Tamamshjan (1959).

** *A. miquelianus* was treated as a species in *Kalimeris* sect. *Cordifolium* by Kitamura.

*** The number of species was estimated from the treatments of Cronquist (1980) and Anderson (1987).

**** Based on Y. L. Chen (1986).

of *Aster* sensu stricto, six Eurasian genera segregated from *Aster*, and *Boltonia*; the results are listed in Table 1.

Asterothamnus, *Galatella*, and *Linosyris* are characterized by their woody habit, unevenly compressed achenes, and multi-seriate pappi. These genera are distributed in northwestern and central Asia and are very distinct from the other groups listed in Table 1. Although *Boltonia* is similar to *Kalimeris* in floral morphology, detailed analyses indicate that the similarity is rather superficial. Both genera have compressed achenes, but the achenes of *Boltonia* are very flat with thin and almost transparent wings (Fig. 1), whereas the achenes of *Kalimeris* are only laterally compressed and have thickened margins (Fig. 2). The "shared" short pappi have been used to support the argument that these two genera should be combined, but on careful examination the pappus bristles of the two genera are rather different. *Boltonia* has pappus bristles of unequal length, and a longer awn is found on each side at the top of the achenes (Fig. 1). *Kalimeris* has subequal pappus bristles or, if unequal, several longer bristles are interspersed with shorter ones (Fig. 2). The texture of the pappus is also different in *Boltonia* and *Kalimeris*: the former has fragile pappi similar to those of *Erigeron*, whereas the latter has robust pappi like those of *Aster* and *Heteropappus*. *Boltonia* also has entire, glabrous leaves and narrow phyllaries with often colored midribs, whereas *Kalimeris* has lobed or incised, variously hairy leaves and broader phyllaries with green midribs. In summary, detailed comparison of the achenes and pappi in *Boltonia* and *Kalimeris* does not support a close relationship between them; most of the purported "similarities" are non-homologous and may reflect convergent evolution, such as that documented in many taxa of Asteraceae by Cronquist (1955) and Stebbins (1977).

Kalimeris was subdivided into two sections by Kitamura (1937b): sects. *Cordifolium* and *Kalimeris* (as *Asteromoea*), which have been adopted by other Asian botanists (e.g., Ling et al., 1985). The only characteristic shared by these two sections is short pappus bristles. They differ in many other funda-

Table 1. Extended.

Receptacle		Ray (achene)		Disc (achene)			Pappus	
Shape	Surface	Shape	No. of ribs	Shape	No. of ribs	Indument	Ray	Disc
flat	smooth	cylindrical	6–8	cylindrical	6–8	glabrous	A	A
convex	alveolar	triangular	3–4	compressed	2–3			
flat ± convex	alveolar	very compressed	2(–3)	very compressed	2	hairy glandular	B–C	A
convex subconical	alveolar	triangular	3(–4)	compressed	2(–3)	hairy glandular	C	C
flat	alveolar	cylindrical	6–7	cylindrical	4–6	glabrous	C	C
conical	smooth	± triangular	3	very flat	2–3	glabrous loosely hairy	D	D
flat ± convex	smooth alveolar	cylindrical ± triangular	5–6 3	cylindrical ± compressed	4–5 2–3	glabrous densely hairy	X	X
convex conical	alveolar	triangular	3	triangular	3	hairy	E	E
flat convex	alveolar scaled	compressed abaxially	1–2	compressed abaxially	1–2	densely hairy	E	E
flat convex	scaled	X	0	compressed abaxially	1–2	hairy	E	E

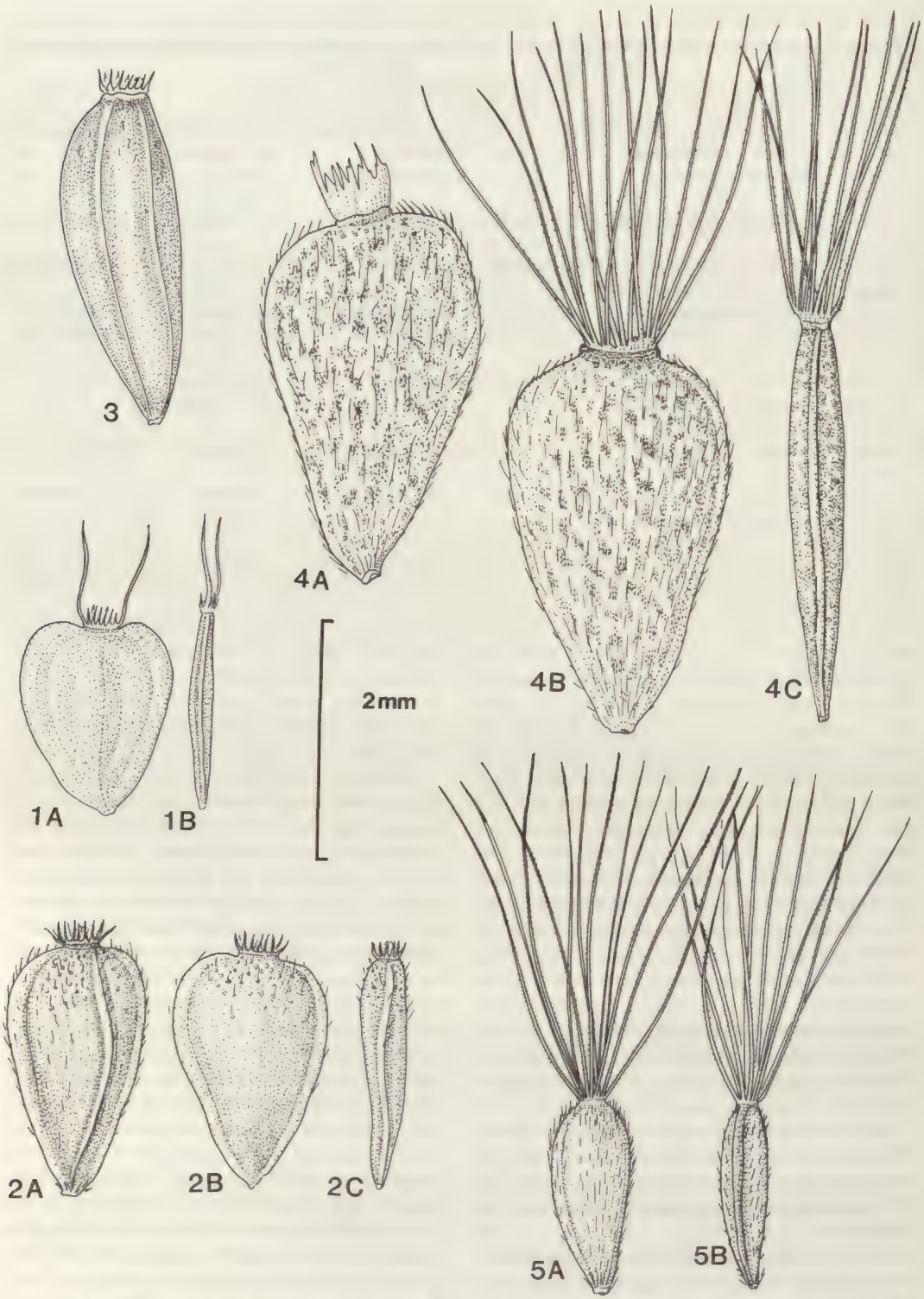
mental characters; for example, species in section *Cordifolium* have cordiform leaves with long petioles, 2–3 series of subequal phyllaries, and cylindrical achenes with 5–7 ribs (Fig. 3, Table 2), whereas species in section *Kalimeris* have oblong and sessile leaves, 3–4 series of imbricated phyllaries, and laterally compressed achenes with 2–3 ribs. Cytological and anatomical evidence also shows that these two sections are very different (Gu, 1987, 1989), and that retention of section *Cordifolium* in *Kalimeris* would make the genus diphyletic. These observations are also supported by evidence from molecular studies on the Japanese taxa of *Kalimeris* and some related *Aster* species (Nishino & Morita, 1994; Ito et al., 1994, 1995). Consequently, section *Cordifolium* is excluded from *Kalimeris* in this treatment and left as part of *Aster*. The relationships of this group remain to be determined.

Although *Miyamayomena* has only five species (Chen, 1986), it is as variable morphologically as the large genus *Aster*, as shown in Table 1. This group may in fact be an artificial assemblage, but further study clearly is needed.

Aster, even when circumscribed in the narrower sense used here, is a very speciose and morphologically diverse genus. Three main subgeneric classifications based only on external morphology are available for Eurasian *Aster* from regional flora treatments (Kitamura, 1937b; Tamamshjan, 1959; Ling et al., 1985). For convenience in the following discussion, I have adopted Ling's system of *Aster*, in which the genus is subdivided into 3 sections, *Aster*, *Orthomeris* A. Gray, and *Alpigenia* Benth., and 27 series.

Kalimeris is most similar to *Heteropappus* and *Aster* (especially sect. *Orthomeris* ser. *Ageratoides* Kitamura). The main differences among these three groups are habitat specialization, habit, leaf and phyllary morphology, and floral and achene morphology (Table 2). Phyllary and achene morphology are the most useful characters for distinguishing the three genera in the field. *Heteropappus* is characterized by its two series of subequal herbaceous phyllaries and dimorphic pappi in the ray and disc achenes: shorter pappi on the ray achenes and longer pappi on the disc achenes (Fig. 4). The unequal corolla lobes have also been used to distinguish *Heteropappus* from the other two genera (Grierson, 1964), although this character state is also found in several species of *Aster* and *Kalimeris*. *Aster* and *Kalimeris* are similar in having 3–4 series of imbricated phyllaries, but differ in that *Aster* has either laterally compressed achenes with pappus bristles of the same length as the disc corollas (Fig. 5) or cylindrical achenes with shorter pappus bristles or none, whereas *Kalimeris* has laterally compressed achenes with short pappus bristles no longer than the length of the corolla tube.

As mentioned earlier, convergent evolution is



Figures 1–5. Morphology of achenes. —1. *Boltonia diffusa*; A. Front view. B. Side view. —2. *Kalimeris indica*; A. Ray achene. B, C. Disc achene of front view and side view, respectively. —3. *Aster miquelianus*. —4. *Heteropappus hispidus*; A. Ray achene. B, C. Disc achene with front view and side view, respectively. —5. *Aster ageratoides*. A. Front view. B. Side view.

Table 2. Character comparison among *Aster* ser. *Ageratoides*, *Heteropappus*, and *Kalimeris*.

Character	*Aster* ser. *Ageratoides*	*Heteropappus*	*Kalimeris*
Habit	perennial	biennial	perennial
Habitat	montane forest or disturbed area	dry, sandy, or saline soil	disturbed area
Root	fibrous	tap	fibrous; tap-root in one species
Underground stem	absent or rhizome	absent	rhizome; absent in one species
Leaf venation	3 basal veins	1 midvein	1 midvein
Phyllaries	3–5 series, imbricate	2 series, subequal	3–4 series, imbricate
Fibers in cross section of phyllary	continuous	separate	continuous
Receptacle	± convex or flat	flat	convex or subconical
Ratio: long/short corolla lobes	1–1.7	1.5–2.4	1–1.8
Achene morphology	± compressed	very compressed	compressed
Ratio: achene length/thickness	2–3.1	6–7.7	3–4.2
Number of ribs on ray achene	3–4	2(–3)	3(–4)
Number of ribs on disc achene	2–4	2	2–3
Ratio of lengths: ray pappus/disc pappus	1	less than 1 (rarely 1)	1 (rarely less than 1)
Relative length of disc pappus	same as disc corolla	same as disc corolla	shorter than disc corolla

common in Asteraceae. In very few cases can a single character be used to delimit a genus. For example, short pappi have evolved many times in different phylogenetic lines in Astereae. Several Asian species of *Aster* with short pappi (e.g., *A. procerus* Hemsl. and *A. smithianus* Hand.-Mazz.) have either been included in *Kalimeris* (Hu, 1967) or (*A. tongolensis* Franch.) proposed for inclusion (Jones & Smogor, 1983), but overall these species share very few other characters with *Kalimeris* and should not be included therein.

Although *Kalimeris* is treated as a distinct genus here, the ranking of this morphologically discrete taxon at the generic level is provisional, to the degree that it ultimately must be consistent with a comprehensive classification of the Astereae.

Materials and Methods

Conventional morphological data were derived from more than 3500 herbarium specimens of Astereae, 2000 of *Kalimeris* and 1500 of other members of the tribe from Asia (*Aster, Asterothamnus, Doellingeria, Galatella, Heteropappus, Linosyris, Miyamayomena,* and *Turczaninowia*) and North America (*Boltonia*). Numbered collections are referenced in a collectors' index. Morphological measurements on this material were supplemented by observations on living plants in the field and in cultivation. Study of the morphology of rosettes was made almost entirely on living plants in the greenhouse. At least ten specimens of each species, from different populations, were measured for morphological characters. The morphological terminology is based mainly on Lawrence (1951). Cauline leaves were measured at the middle portion of the stem; if the leaves in that portion were withered, the leaves below the lowest branch were measured. Floral features were measured on fully opened flowers, as indicated in Figure 6.

We have adopted the "morphological species concept" (Davis & Heywood, 1963; Stuessy, 1990) in *Kalimeris* as the most practical approach in this variable group. Our species are definable by morphology, with sharp discontinuities between species; where possible, each is defined by one or more autapomorphies. For taxa whose morphological discontinuity is correlated with ploidy levels and/or with allopatry, but where substantial intergradation may occur in areas of overlap, we have used the category of subspecies (Raven & Raven, 1976).

Morphology and Taxonomic Characters

The eight species of *Kalimeris* are distinguished by combinations of characters, and many of the features differ only quantitatively. In the following text, a description of general morphological characters is provided, with emphasis on some characters useful in classification.

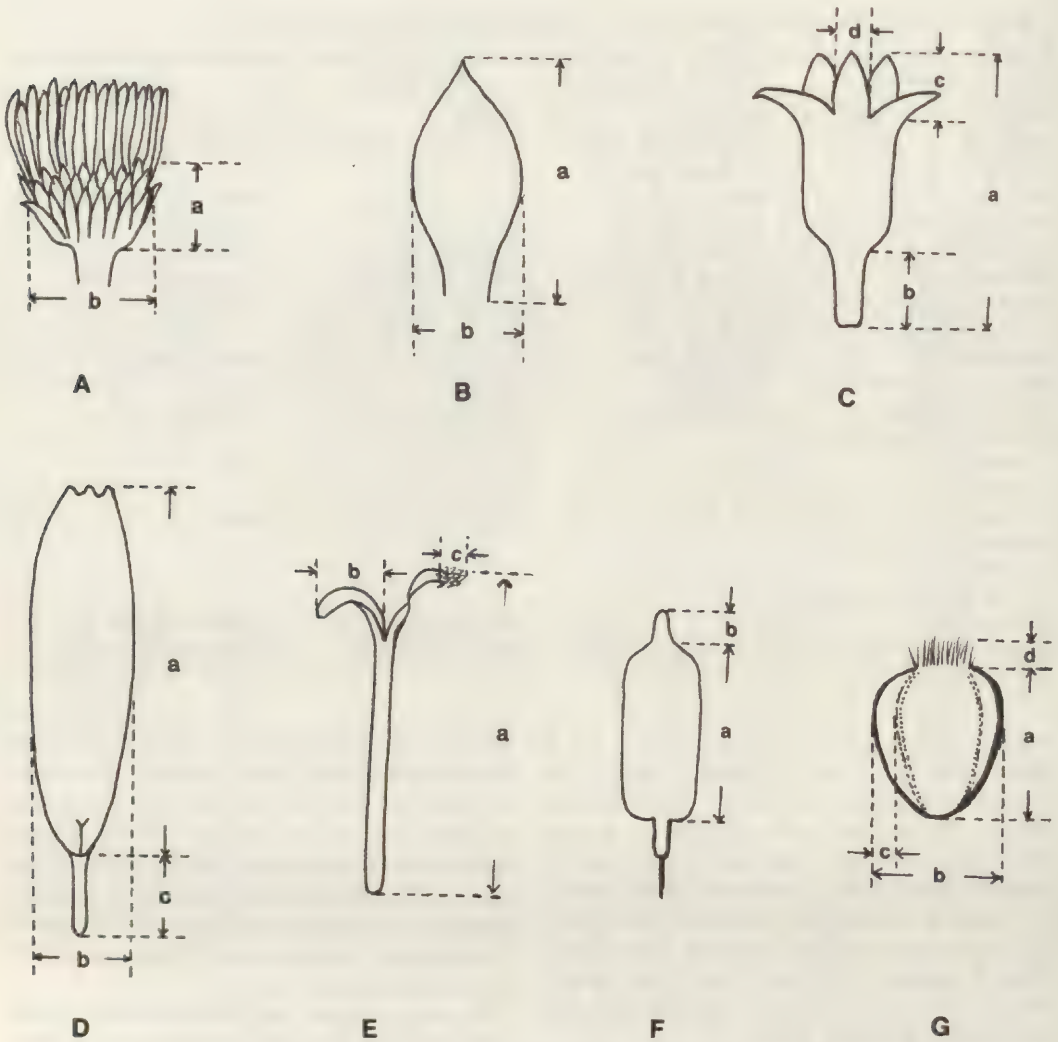


Figure 6. Diagram of floral parts measured. —A. Length (a) and width (b) of involucre. —B. Length (a) and width (b) of phyllary. —C. Length of disc floret (a) and corolla tube (b); length (c) and width (d) of corolla lobe. —D. Length (a) and width (b) of ligule of ray floret; length (c) of corolla tube. —E. Length of style (a), style branch (b), and style appendage (c). —F. Length of anther (a) and anther appendage (b). —G. Length (a) and width (b) of achene; width of the margin of achene (c); length of pappus (d).

HABIT AND LIFE HISTORY

All species of *Kalimeris* are perennial herbs. Rosettes grow out from winterized underground stems (rhizomes) or adventitious buds in early spring, and stems shoot out from the rosettes in late spring. Prior to flowering, branches begin to develop from the uppermost lateral buds, and the lower branches develop subsequently from the lateral buds below the first branch on the main stem. Generally the flowering period begins in late May and ends in early November. The species in the northern part of the range, e.g., *K. incisa* and *K. pinnatifida*, usually bloom from late June to October, while southern species, such as *K. indica* and *K. shimadai*, bloom for a longer period from May to November. Achenes begin to mature in most areas by late September. The main stem dies back in winter and the plants perennate from underground stems and adventitious buds.

STEMS AND BRANCHES

All species have erect and herbaceous stems 10–200 cm tall. The stems are usually ridged and greenish, sometimes purplish in *K. indica*, and covered with ascending, nonglandular, uniseriate-multicellular hairs interspersed with biseriate glandu-

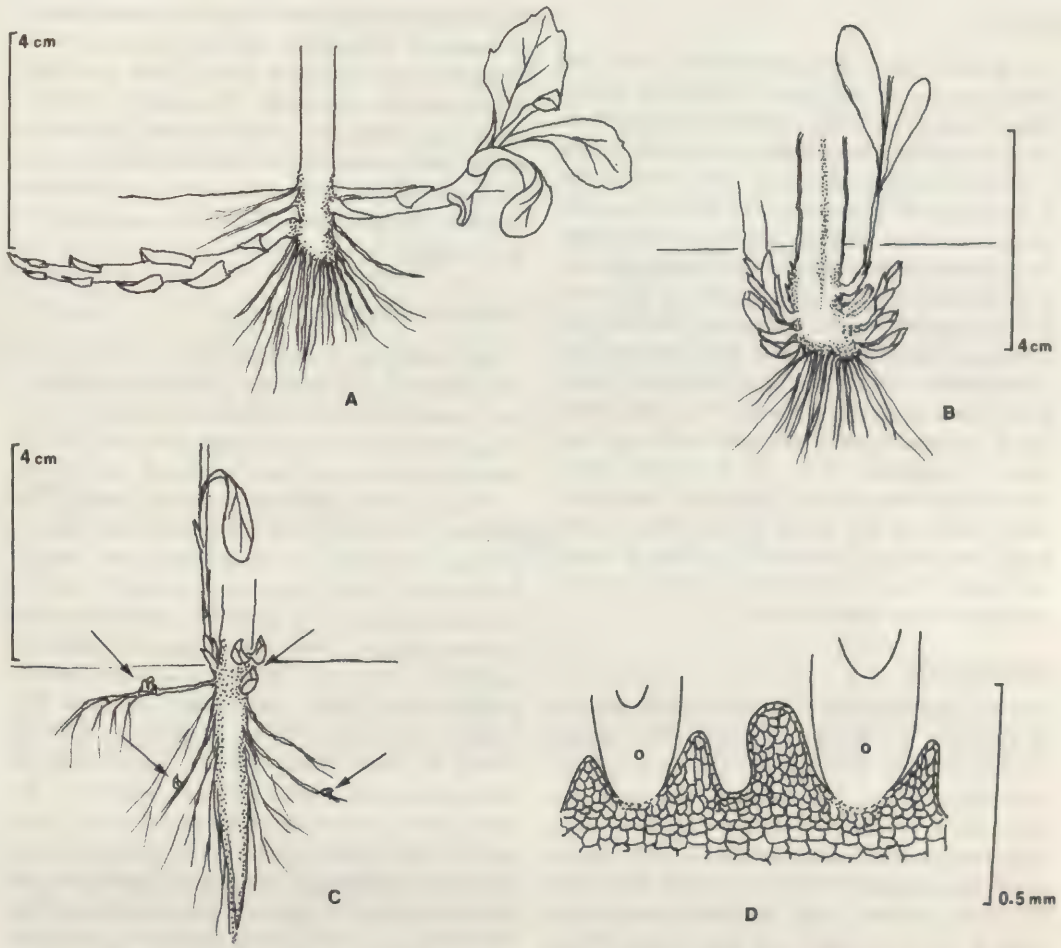


Figure 7. Perennating structures and cross section of a receptacle. —A. Stoloniferous rhizome (*K. yomena* subsp. *yomena*). —B. Condensed rhizome (*K. lautureana* subsp. *lautureana*). —C. Adventitious buds (arrows, *K. integrifolia*). —D. Cross section of a receptacle showing alveolar surface.

lar hairs. The hairs are deciduous or restricted to the ridges on the lower stems and become denser upward. The vigorous growth of branches begins when the main stem is terminated by a capitulum. The angles between the branches and the main stem are usually less than 45°, with the exception of *K. incisa* subsp. *macrodon* and *K. indica* subsp. *collina*, in which the angles are greater than 45°. Tertiary branches are formed when the secondary branches are terminated by a capitulum.

ROOT SYSTEM AND UNDERGROUND PERENNATING STRUCTURES

All species have a fibrous root system, with the exception of *K. integrifolia*, which has a tap-root system. Stoloniferous rhizomes, i.e., underground stems with long internodes, are formed prolifically in *K. indica*, *K. pinnatifida*, and *K. yomena* during the flowering season and are characterized by internodes 5–10 mm long, with whitish scales at the nodes (Fig. 7A). Condensed rhizomes, usually with thicker stems and shorter internodes, are found in *K. incisa*, *K. mongolica*, *K. lautureana*, and *K. shimadai*. They sometimes have almost indistinguishably short internodes, and usually form big rootstocks (Fig. 7B). *Kalimeris integrifolia* is characterized by formation during the flowering season of adventitious buds from the lateral roots or near the top of the main root (Fig. 7C). These rhizomes and adventitious buds either develop into non-reproductive shoots in the same season, or remain dormant underground and grow out the following spring.

LEAVES

Leaf morphology varies greatly both among and within species in this genus. During the rosette stage, leaves are usually narrowly oblanceolate or linear in *Kalimeris integrifolia,* and obovate, broadly oblanceolate, or spathulate in other species, none of which can be distinguished by this feature. The margin is ciliate, serrate, crenate, or sometimes deeply lobed on most species, but always entire in *K. integrifolia.* The leaf apex is acute or obtuse or, in upper cauline leaves, acuminate. The leaf base is attenuate into a short petiole 5–20 mm long. The indumentum is similar to that of the cauline leaves of the same individual in most of the taxa, except that *K. lautureana* and *K. shimadai* have longer and denser nonglandular hairs on the rosette leaves than on the cauline leaves. The rosette leaves gradually wither as the stems mature. The cauline leaves are obovate, oblanceolate, oblong, or linear, and sessile. The leaves below the lowest branches gradually wither after anthesis.

INFLORESCENCE

As in most genera of Astereae, the inflorescence in *Kalimeris* is a radiate capitulum. The capitula always terminate the stems and branches, and are cymosely arranged. The corollas of the fertile pistillate ray florets are whitish, light purple, or lilac (but never yellow), and consist of a tube and an oblanceolate ligule 5–28 mm long with three shallow distal notches. In the ray florets, the androecium is absent or rarely with 3–4 nonfunctioning anthers (or usually just remnant filaments) in the tube; the gynoecium comprises an inferior ovary with three vascular bundles and a single style with two branches at the top. The lower portions of the branches are stigmatic in function, and the style always exceeds the corolla tube at receptivity.

The disc florets are bisexual, fertile, and always yellow. The corolla throat is campanulate, abruptly narrowed at the base into a tube, and 5-lobed distally. The lobes are triangular or broadly lanceolate and usually ⅓–½ the length of the throat. The androecium is syngenesious, i.e., the five anthers are united laterally and their filaments are distinct. The filaments are glabrous and adnate to the corolla tube alternate with the lobes. The anthers are truncate distally with triangular appendages. The gynoecium is the same as that of the ray florets except that the ovary has two lateral vascular bundles.

PEDUNCLE

The peduncles in *Kalimeris* are 0.3–18 cm long. They are usually covered densely with the same kind of nonglandular hairs as on the stems, and in *K. indica, K. integrifolia,* and *K. shimadai* are interspersed with glandular hairs. There are 1–13 bracts along the peduncles. The number of bracts varies both among and within species. The bracts on the lower peduncles are similar to the leaves on the branches, and those on the upper peduncles are similar to the phyllaries of the outermost whorl of the involucre.

INVOLUCRE AND PHYLLARIES

The involucre is hemispheric or campanulate and composed of 3–4 whorls of imbricated phyllaries. Generally, it is 4.5–13 mm wide and 3.5–9 mm long, although smaller involucres are found in *Kalimeris integrifolia,* and larger ones in *K. mongolica.*

The size of the phyllaries increases inward. The smallest phyllaries, those in the first whorl, are triangular, lanceolate, or oblanceolate, and usually herbaceous. The phyllaries in the middle whorl(s) are oblong, obovate, or spathulate, and have membranous margins. Some individuals of *Kalimeris mongolica* have very broadly spathulate middle phyllaries with broad, membranous margins. The texture of the phyllaries varies from herbaceous (*K. incisa*) to almost chartaceous (*K. integrifolia*). In other species, the phyllaries are herbaceous on the upper green portion and chartaceous on the lower portion. The longest phyllaries, those of the inner whorl, are oblong, oblanceolate, spathulate, or sometimes linearly oblong, or linearly oblanceolate. Phyllaries in all whorls have ciliate and sometimes purplish margins.

RECEPTACLE

All species in *Kalimeris* have convex or subconical and alveolate receptacles 1.1–2.8 mm wide and 0.5–2.2 mm high. The alveolate appearance is caused by the outgrowth of the epidermal cells and a few layers of cells beneath them around the attachment of achenes (Fig. 7D).

INDUMENTUM

The nonglandular trichomes on the leaves and stems comprise multicellular and uniseriate hairs. Both the type and the density of these hairs have been used in distinguishing species within the genus. For the convenience of this discussion, they are termed thin or thick ascending hairs and appressed hairs. The thin ascending hairs are composed of 4–6 long rectangular cells slightly swollen at the top and bottom, and without a prominent base (Fig. 8A); the thick ascending hairs are com-

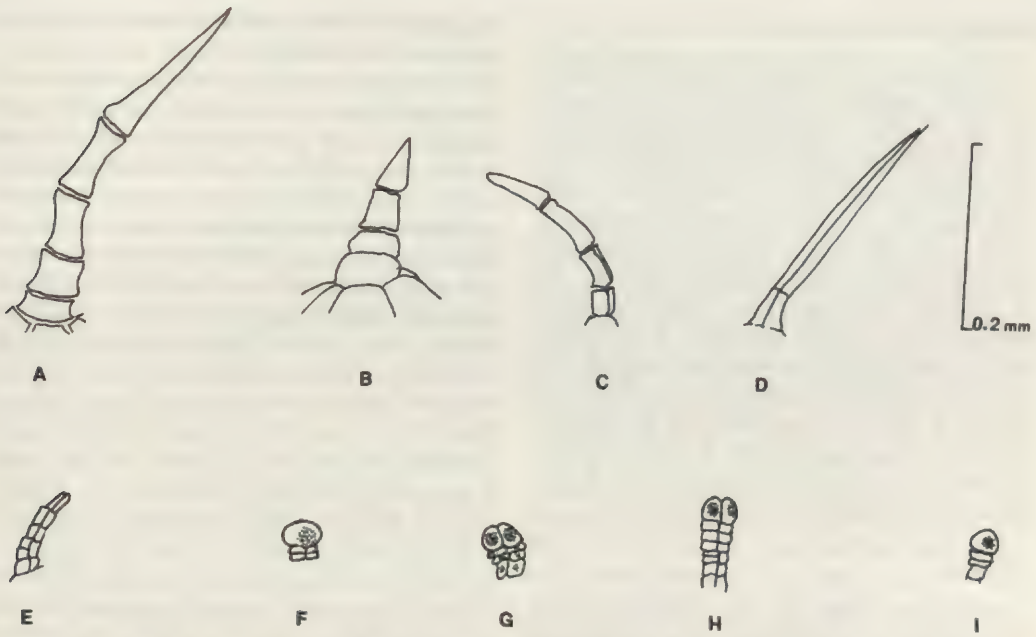


Figure 8. Types of trichomes. —A. Thin ascending nonglandular hair (*K. shimadai*). —B. Thick ascending nonglandular hair (*K. indica* subsp. *indica*). —C. Prostrate nonglandular hair (*K. integrifolia*). —D. 4-celled nonglandular hair (*K. indica* subsp. *indica*). —E. Biseriate nonglandular hair (*K. indica* subsp. *indica*). —F. Biseriate, one-cell-tipped glandular hair (*K. integrifolia*). —G. Biseriate, two-cell-tipped glandular hair (*K. indica* subsp. *indica*). —H. Biseriate, two-cell-tipped, long-stalked glandular hair (*K. pinnatifida*). —I. Uniseriate glandular hair (*K. yomena* subsp. *yomena*).

posed of 2–4 short rectangular cells and a prominent base of several epidermal cells (Fig. 8B); and the appressed hairs are composed of 3–5 rectangular cells without prominent bases (Fig. 8C). Thick ascending hairs are scattered on the leaves of *Kalimeris indica* subsp. *indica*, *K. incisa*, *K. pinnatifida*, *K. mongolica*, and *K. yomena* and densely cover the leaves of *K. indica* subsp. *collina*. *Kalimeris indica* subsp. *stenolepis* and *K. shimadai* are characterized by thin ascending hairs densely covering the leaves. The leaves of *K. integrifolia* are densely covered with appressed hairs.

The nonglandular hairs on the achenes are 4-celled, biseriate, and ascending (Fig. 8D) and are found in all species except *Kalimeris integrifolia*. In *K. indica*, the basal cells of these hairs are usually brownish. The nonglandular hairs on the corolla are biseriate and multicellular (Fig. 8E).

There are two kinds of stipitate glandular hairs on leaves. One type has several flat cells at the base in two series and one large flat secretory cell at the tip (Fig. 8F), and the other type has several cells in two series at the base and two swollen secretory cells at the tip (Fig. 8G). Both types are found on the leaves of *Kalimeris indica*, *K. integrifolia*, *K. pinnatifida*, and *K. shimadai*. Two somewhat different kinds of glandular hairs are found on the corolla of ray and disc florets of all species in the genus. One type is a biseriate hair with a long stalk and two secretory cells at the tip (Fig. 8H), and the other is a uniseriate hair with one large secretory cell at the tip (Fig. 8I).

PAPPI

Pappus morphology has been used as one of the main characters in previous infrageneric classifications of *Aster* sensu lato. The pappus bristles of *Kalimeris* are composed of elongated, lignified cells; they are usually 2–12 cells thick at the base, and multicellular in length. They tend to unite at the base in *K. integrifolia*, *K. lautureana*, and *K. shimadai*, but are separated in the rest of the species. The pappus bristles range from 0 to 1.5 mm long, with *K. incisa* and *K. mongolica* having particularly long bristles (0.6–1.5 mm long); epappose individuals are often found in *K. indica* subsp. *indica*, and rarely in *K. shimadai* and *K. integrifolia*. Some individuals of *K. incisa*, *K. integrifolia*, *K. mongolica*, and *K. shimadai* have ray pappi shorter than disc pappi.

ACHENES

The achenes are laterally compressed, obovate or broadly obovate. The disc achenes have two lateral ribs (vascular bundles) or occasionally three. The ray achenes in all species of *Kalimeris* are 3(–4)-ribbed, with 2(–3) ribs abaxially and 1 adaxially (e.g., Fig. 3), and are isosceles-triangular in cross section. The achenes are purple or dark purple in *K. indica*, *K. pinnatifida*, *K. shimadai*, and *K. yomena*, and gray-green, straw-colored, or brownish in *K. incisa*, *K. integrifolia*, *K. lautureana*, and *K. mongolica*. The achenes have a whitish margin 0.1–0.4 mm wide. Glandular hairs are found at the top of the achenes commonly in *K. indica*, *K. integrifolia*, *K. pinnatifida*, and *K. yomena*, and occasionally in some individuals of *K. incisa*, *K. lautureana*, *K. mongolica*, and *K. shimadai*.

Cytology

The basic chromosome number of *Kalimeris* is $x = 9$. All eight species recognized in this treatment were examined cytologically (Gu, 1989; Gu & Tara, 1990). Two tetraploid, a hexaploid, and three 12-ploid taxa were counted for the first time in this genus.

Geographic Distribution

Kalimeris is native to East Asia, ranging from the Amur Basin of northeastern China and adjacent Russia, Korea, and Japan, through central and southern China to northern Vietnam, Thailand, and Burma. Most species have more limited ranges within this region.

Kalimeris incisa and *K. mongolica* have the northernmost distribution, occurring in the humid temperate region along the Amur and Ussuri Rivers and reaching Blagoveshchensk in Russia, the northeastern limit of the genus. Both species also occur in Korea, *K. incisa* from the Chinese border to Cheju Island of South Korea and through the western plains regions. *Kalimeris mongolica* is here correctly attributed to Korea for the first time; prior to this, it was misidentified as *K. lautureana* (e.g., in the *Flora of Korea*; Nakai, 1911). *Kalimeris lautureana* is endemic to China and has a narrower geographic distribution than usually has been attributed to it, due to taxonomic confusion with *K. mongolica*. *Kalimeris shimadai* is also endemic to China and occurs abundantly on the Loess Plateau and scattered throughout subtropical central and southern China, extending to northern Taiwan.

Kalimeris integrifolia and *K. indica* are the two most widely distributed species. The former occurs abundantly from the Amur Basin to Korea and central China, with its southern limit in Jiangsu and Anhui provinces, and its southwestern limit in Sichuan and Yunnan provinces. It is sympatric with several species: *K. incisa* and *K. mongolica* in the northern part, and *K. indica* and *K. shimadai* in the southern part. *Kalimeris indica* occurs in central and South China and northern Taiwan, and extends to the Ryukyu Islands and southern Kyushu of Japan, and to southern Korea. It reaches its southern limit in the plains regions of northern Vietnam and Burma, and its northern limit at the northern base of the Qinling Mountains and the southern edge of the Loess Plateau in the Weihe and Fenhe Valleys, where the original warm temperate forest-steppe vegetation has been mostly removed by cultivation. It is recorded from India, Indonesia (Java, Sumatra), and Malaysia (Malacca), where it may have been cultivated originally for its edible rosettes, medicinal uses, or ornamental purposes (Miquel, 1856), but it escaped from cultivation and has become naturalized in these areas. The recent collection from Oahu, Hawaii Islands, also certainly reflects an introduction, perhaps through commercial horticulture or by accident.

Japan has two endemic species, *Kalimeris pinnatifida* and *K. yomena*. The former occurs in southern Hokkaido, extending south to the main island of Honshu, with its southern limit in northern Kinki District (Kyoto, Nara, and Mie). *Kalimeris yomena* is distributed from Niigata of northern Chubu District to Shikoku, Kyushu, and the Ryukyu Islands.

Altitudinal Distribution

All of the species of *Kalimeris* are found at elevations below 900 m, but some species can also grow as high as 2600 or 3100 m (*K. lautureana* or *K. indica*, respectively) in the mountains and plateaus of central and southwestern China.

Habitat

All of the species of *Kalimeris* grow in relatively disturbed habitats. They are basically heliophytes and are usually associated with human activities. They grow in sunny and dry places along roadsides, at the edges of crop fields, or on abandoned lands. Sometimes they are found in relatively mesic areas on the floor of open forests. For example, *K. incisa* and *K. mongolica* grow inside the temperate secondary-growth forests in the northern part of the range of the genus, and at low elevations in montane regions in meadows and at the margins of mixed coniferous and broad-leaved forests. *Kali-*

meris indica subsp. *stenolepis* grows along margins of subtropical mixed deciduous and evergreen broad-leaved forests in the southern part of the range. *Kalimeris indica* has the broadest ecological range in the genus, occurring from cool, humid temperate to warm subtropical regions at margins of cliffs, in poor, often disturbed soils, at margins or inside of open forests and thickets, or near crop fields. *Kalimeris integrifolia* is usually found in relatively disturbed areas, and especially when it is sympatric with other *Kalimeris* species, it always occurs in more disturbed habitats.

Systematics of *Kalimeris*

Kalimeris (Cass.) Cass., in F. Cuvier, Dict. sci. nat. 37: 464, 491. 1825. *Aster* subg. *Kalimeris* Cass., in F. Cuvier, Dict. sci. nat. 24: 324. 1822. *Kalimeris* sect. *Kalimeris* Ling, in Y. Ling et al., Fl. reipubl. popularis sin. 74: 99. 1985. TYPE: *Kalimeris platycephala* Cass. ex Nees, nom. illeg. [= *K. incisa* (Fisch.) DC.].

Asteromoea Blume, Bijdr. 907. 1826. *Boltonia* sect. *Asteromoea* (Blume) Benth. in Benth. & Hook. f., Gen. pl. 2: 269. 1873. *Aster* sect. *Asteromoea* (Blume) Makino, Bot. Mag. (Tokyo) 12: 60. 1898. *Kalimeris* sect. *Asteromoea* (Blume) Kitamura, Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 13: 305. 1937. TYPE: *Asteromoea indica* (L.) Blume [= *K. indica* (L.) Sch. Bip.].

Hisutsua DC., Prodr. 6: 44. 1838. TYPE: *Hisutsua cantoniensis* (Lour.) DC. [= *K. indica* (L.) Sch. Bip.].

Martinia Vaniot, Bull. Acad. Int. Géogr. Bot. 12: 31. 1903. TYPE: *Martinia polymorpha* Vaniot [= *K. indica* (L.) Sch. Bip.].

Perennial erect herbs. Root system fibrous or tap-root; perennating by condensed or stoloniferous rhizomes and adventitious buds from main or lateral roots. Stem forming from rosettes prior to flowering, (10–)20–200 cm tall, cymosely branched, ridged, covered with ascending or appressed, uniseriate nonglandular hairs, these denser along the prominent ridge lines, sometimes interspersed with biseriate or uniseriate, glandular hairs; the lower part usually glabrous and not ridged, or rarely with scattered nonglandular hairs after anthesis; branches up to 48 cm long, the angle between the branches and the stem usually less than 45° or sometimes greater than 45°. Rosette leaves oblong, oblanceolate, or broadly obovate, less often narrowly oblanceolate, (3.5–)4.5–11 × (1.2–)2.5–4.4 cm, glabrous to densely covered with nonglandular hairs, the apex acute or obtuse, the margin ciliate, remotely crenate, serrate to deeply serrate, or sometimes entire, the base attenuate or reduced abruptly to petiole 0.5–2 cm long, withering after the stem has formed; cauline leaves alternate, linear, narrowly oblong, or oblanceolate to obovate, the margins ciliate, serrate to deeply pinnate-lobed, or less often entire; gradually reduced in size upward, those on the lower stem usually withering after anthesis, the upper ones (0.7–)3.5–11(–15) × (0.2–)0.5–2.5(–3.5) cm, glabrous to densely covered with thin or thick multicellular, nonglandular hairs and interspersed with biseriate, 1–2-cell-tipped glandular hairs, usually denser on the abaxial surface or sometimes restricted to the veins, the apex acuminate, acute, or obtuse, the base attenuate or cuneate, sessile. Capitula (5–)10–120(–200), terminating the stems or branches, loosely cymosely arranged; peduncle (0.3–)2.5–12(–18) cm long, often densely covered with ascending, thin, multicellular, nonglandular hairs and interspersed with biseriate, glandular hairs; bracts 1–10(–13) along the peduncle, the lower ones leaf-like, narrowly oblong, oblanceolate, or lanceolate, entire, 6.1–16(–30) × 0.7–3.2(–8) mm, the upper ones phyllary-like, linear to oblanceolate, 1.2–4.5(–8) × 0.2–1.4(–2.5) mm; involucre hemispherical or campanulate, 4.5–13 mm broad, 3.5–6.5(–9) mm high. Involucral phyllaries in 3–4 loosely or tightly imbricated whorls, gradually increasing in size inward, the distal part of phyllaries usually herbaceous and green, the proximal part chartaceous and whitish, the abaxial surface glabrous to densely covered with nonglandular hairs and sometimes interspersed with biseriate, glandular hairs, the adaxial surface usually glabrous or rarely with scattered, thin, nonglandular hairs, the margins ciliate and membranous, sometimes purplish; phyllaries of the outermost whorl lanceolate or obovate, (1.5–)2.5–5(–7.2) × 0.5–1.8(–2.8) mm, the apex acute, obtuse, or sometimes acuminate (*K. integrifolia*); those of the middle whorl(s) oblong, obovate, or spathulate, 2.3–6.4(–8.1) × (0.7–)0.9–3(–3.5) mm, the apex acute, obtuse, or acuminate; those of the inner whorl(s) oblong, obovate, or spathulate, (3–)4–7(–8) × (0.6–)0.8–2.5(–3.2) mm, the apex acute, obtuse or acuminate. Receptacle convex or occasionally subconical, alveolate, 1.1–2.8 mm wide, 0.5–2(–2.2) mm high. Ray florets pistillate, confined to the periphery of the capitulum, 10–30; corollas whitish to light purple, ligules narrowly oblong, oblanceolate, or less often elliptical, (5.2–)6.6–22(–28) × 1.1–4.5(–5.2) mm, the apex obtuse with three very small notches, the tube 0.7–2.6 mm long, covered with biseriate nonglandular and glandular hairs; style exceeding the corolla tube, 1.3–3.4(–4.5) mm long, glabrous, the two style branches linear, (0.4–)0.6–1.1(–1.5) mm long. Disc florets bisexual, yellow, (30–)45–115; corollas (2.1–)2.5–5(–

5.8) mm long, the throat campanulate, with 5 broadly lanceolate or triangular, equal, subequal, or unequal lobes each (0.4–)0.7–1.8(–2.2) × 0.4–0.7(–0.8) mm, abruptly narrowed below into a tube 0.6–2 mm long, ½–⅓ as wide as the throat, covered with biseriate glandular hairs; androecium syngenesious, with five anthers 0.7–1.8(–2.2) mm long, each with a triangular or broadly lanceolate appendage 0.2–0.5 mm long; style 1.5–5 mm long, the two branches linear, (0.4–)0.6–1.2(–1.6) mm long, the lower part with marginal stigmatic lines and the upper part topped by two triangular or broadly lanceolate appendages 0.2–1.6 mm long, these covered with collecting hairs on the outer surface and glabrous on the inner surface. Ray and disc pappus bristles uniseriate, whitish to reddish brown, equal or unequal; ray bristles (0–)0.1–0.8(–1) mm long; disc bristles (0–)0.1–0.8(–1.5) mm long. Achenes straw-colored to dark purple, or greenish, obovoid to broadly obovoid, compressed laterally, loosely covered with biseriate, 4-celled, nonglandular hairs and interspersed with biseriate, glandular hairs apically, or with only glandular hairs at the top; the margins light-colored, ciliate, thickened, 0.1–0.4 mm wide; ray achenes 3(–4)-ribbed, 1.5–3.2 × 0.6–1.5(–2.2) mm; disc achenes 2(–3)-ribbed, 1.5–3.2(–3.5) × (0.7–)1.1–2.1(–2.9) mm. Chromosome number: $x = 9$, with aneuploids commonly found in *K. yomena*.

Phenology. Flowering period from late May to November.

Typification of this generic name is problematic. When Cassini published *Aster* subg. *Kalimeris* in 1822, he ascribed to it only one species using the illegitimate combination *Kalimeris platycephala*. In 1825, he elevated this subgenus to a genus, *Kalimeris* (Cass. in F. Cuvier) Cass. in F. Cuvier, but no species was transferred (see King & Dawson, 1975). Unfortunately, no specimens that were possibly used by Cassini have been located. *Kalimeris platycephala* Cass. in F. Cuvier ex Nees (1832) was validly published but with synonymy including earlier species names, e.g., *Grindelia incisa* (Fisch.) Spreng., *Aster tataricus* L. f. (as *A. tartaricus*), *A. incisus* Fisch., and *A. sibiricus* Hort. plurr. It is clear that *K. platycephala* was an illegitimate name then because all other specific names included in the synonymy were earlier, validly published names. The correct name Nees should have used for that species was *K. tatarica*, because *A. tataricus* L. f. (1782) is the oldest name (Article 11.4, *International Code of Botanical Nomenclature*, Greuter et al., 1994). But *A. tataricus* and *A. sibiricus* have different morphological characters than the plant originally described as *K. platycephala* and thus are in conflict with it, and they both are treated as species of *Aster* by contemporary botanists (Kitamura, 1937b; Tamamshjan, 1959; Ling et al., 1985). Because *K. platycephala* is neotypified in this treatment (see the discussion under *K. incisa*), Cassini's designation of the type of the genus *Kalimeris* is followed here.

Key to the Species of *Kalimeris*

1a. Disc pappus bristles more than 0.6 mm long.
- 2a. Branches usually flexible; rhizomes stoloniferous; native in Japan ..... 5. *K. yomena*
- 2b. Branches stiff; rhizomes condensed; native in southeast Russia, China, and Korea.
  - 3a. Phyllaries herbaceous, acute, narrowly lanceolate or oblanceolate ..... 1. *K. incisa*
  - 3b. Phyllaries chartaceous below, blunt, broadly obovate ..... 3. *K. mongolica*

1b. Disc pappus bristles less than 0.6 mm long.
- 4a. Leaves entire, narrowly oblong to oblanceolate, densely covered with appressed, uniseriate, nonglandular and biseriate, glandular hairs ..... 8. *K. integrifolia*
- 4b. Leaves crenate to deeply lobed, rarely entire, oblong, oblanceolate, or lanceolate, glabrous or covered with ascending uniseriate, nonglandular and biseriate, glandular hairs.
  - 5a. Phyllaries acute at apex, mostly 1–1.8 mm long, nearly completely herbaceous ..... 2. *K. pinnatifida*
  - 5b. Phyllaries usually obtuse at apex, mostly 1–2.5 mm long, the upper half herbaceous, the lower portion chartaceous.
    - 6a. Disc pappus bristles less than 0.4 mm long, the bases usually separate; rhizomes stoloniferous.
      - 7a. Pappus bristles 0–0.3 mm long, or, if 0.4 mm, leaves densely covered with nonglandular and glandular hairs adaxially; widely distributed ..... 4. *K. indica*
      - 7b. Pappus bristles 0.3–0.4 mm long; leaves with scattered nonglandular hairs adaxially; native in Japan ..... 5. *K. yomena*
    - 6b. Disc pappus bristles 0.4–0.6 mm long, rarely wanting, the bases united; rhizomes condensed.
      - 8a. Leaves variously lobed, densely covered with glandular and thin ascending, nonglandular hairs ..... 6. *K. shimadai*
      - 8b. Leaves entire to deeply lobed, glabrous or sparsely covered with thick, ascending, nonglandular hairs ... 7. *K. lautureana*

1. **Kalimeris incisa** (Fisch.) DC., Prodr. 5: 258. 1836 ["*Calimeris*"]. *Aster incisus* Fisch., Mém. Soc. Imp. Naturalistes Moscou 3: 76. 1812. *Grindelia incisa* (Fisch.) Spreng., Syst. veg. 3: 575. 1826. *Heteropappus incisus* (Fisch.) Siebold & Zucc., Fl. jap. fam. nat. 1: 182. 1843. *Boltonia incisa* (Fisch.) Miq., Ann. Mus. Bot. Lugduno-Batavum 2: 170. 1866. *Asteromoea incisa* (Fisch.) Koidz., Bot. Mag. (Tokyo) 37: 56. 1923. TYPE: Russia."Aster incisa, Sibiria," "*Fisch.* = Calimeris i. *DC.*" (lectotype, here designated, LE).

Kalimeris platycephala Cass. ex Nees, Gen. sp. Aster. 226. 1832 ["*Calimeris*"]. TYPE: Russia. Amur: Blagoveschensk, *Karo 182* (neotype, here designated; isoneotypes: BM, E, G (three sheets), K, P).

Root fibrous; rhizomes condensed, forming rootstocks up to 3 cm diam. Stem 30–120 cm tall, covered with ascending, uniseriate, nonglandular hairs. Cauline leaves narrowly oblong to obovate, serrate, crenate, or deeply pinnate-lobed, rarely entire, (2.6–)3.6–8(–10) × 0.7–2.4(–3.4) cm, glabrous or with scattered ascending nonglandular hairs adaxially, sparsely to evenly pubescent abaxially (mostly along the veins). Capitula 10–55; peduncles (1.8–)4–14(–18) cm long; bracts 1–9 along the peduncle, the lower ones narrowly to linearly oblong, 8–26 × 1–3(–6) mm, the upper ones linear, (2.1–)3.4–8 × 0.3–1.4(–2.5) mm; involucre hemispherical, 7–11 mm broad, 5–7.5 mm high. Phyllaries in 3–4 whorls, imbricate, covered with short hairs or glabrous, the upper ½–⅔ part of the phyllaries or sometimes the entire phyllaries herbaceous and green, the lower part chartaceous, the margins ciliate and membranous, sometimes purplish; those of the outermost whorl narrowly oblong or lanceolate, (2.5–)3.5–5(–5.2) × (0.7–)0.9–1.4 mm, apex acute, those of the middle whorl(s) oblanceolate, (4–)4.2–5.5(–6.4) × 1.6(–2) mm, the apex acute, those of the inner whorl oblanceolate to oblong, (4.3–)4.7–6(–6.5) × 1.1–1.8(–2.2) mm, the apex acute. Receptacles convex or subconical, (1.1–)1.5–2.4 mm wide, (0.7–)1.2–2.1 mm high. Ray florets (13–)16–27(–29); corollas pale lilac to pale purple, ligules narrowly oblong or oblanceolate, (8.5–)11.5–20(–22) × (1.8–)2–2.8(–3.2) mm, the tube (0.9–)1.1–1.6 mm long; style (1.6–)1.9–2.8 mm long, the branches 0.7–1.2 mm long. Disc florets (40–)58–115; corollas 3–4(–4.2) mm long, the lobes unequal, the longer one 0.9–1.6(–2) mm long, the shorter ones 0.6–1.2(–1.5) mm long, both 0.3–0.6 mm wide; tube (0.6–)0.9–1.3(–1.5) mm long and usually covered with biseriate, nonglandular or glandular hairs; anthers 0.9–1.4(–1.6) mm long; style 2.5–4.3 mm long, the branches 0.8–1.3 mm long, each with a triangular appendage 0.3–0.4 mm long. Ray and disc pappus bristles whitish to light brown, sometimes unequal; ray bristles (0.2–)0.5–0.8(–1) mm long; disc bristles (0.5–)0.6–1.1(–1.5) mm long. Achenes greenish to straw-colored, obovate to broadly obovate, covered with 4-celled, biseriate, nonglandular hairs or these sometimes interspersed with biseriate, glandular hairs at the top, the margins 0.2–0.4 mm broad; ray achenes 3-ribbed, 2.6–3.1 × 1.1–1.5 mm; disc achenes 2-ribbed, 2.6–3.1 × 1.4–2 mm. Chromosome number: $n = 9$. Figure 9A–D.

Phenology. Flowering period: late June to October.

From the two specimens Tamamshjan (1959) selected as the type of *Kalimeris incisa*, the one with the annotated label "Aster incisa, Sibiria" and an added note "Fisch. = Calimeris i. DC" is chosen as the lectotype for *K. incisa* here. The type specimen of *K. platycephala* was based on a cultivated strain labeled as *Aster sibiricus* from the "Jardin du Roi," now the Muséum National d'Histoire Naturelle in Paris. No authentic specimens have been located. In order to follow the typification of the genus *Kalimeris* made by the first author, Cassini in this case, a well-duplicated specimen collected by F. Karo is selected as the neotype of *K. platycephala* here (Greuter et al., 1994: Article 9.6 and 9.11).

This species has the most northeastern distributional range in the genus and is divided into two subspecies: subsp. *incisa* and subsp. *macrodon*.

KEY TO THE SUBSPECIES OF *KALIMERIS INCISA*

1a. Branches usually diverging from the stem by less than 45°; leaves oblanceolate to narrowly oblong, serrate, or rarely entire; ray corolla 15.5–22 mm long ..... 1a. subsp. *incisa*

1b. Branches usually diverging from the stem by more than 45°; leaves oblong to elliptic, crenate; ray corolla 8.6–15.5(–16) mm long ..... 1b. subsp. *macrodon*

1a. **Kalimeris incisa** subsp. **incisa**

Aster incisus var. *australis* Kitag., Rep. Inst. Sci. Res. Manchoukuo 1: 323. 1936. *Kalimeris incisa* var. *australis* (Kitag.) Kitag., Neo-lin. fl. Manshur. 652. 1979. TYPE: China. Jilin: Wui-hu-lin Railway Station, 2 Sep. 1936, *M. Kitagawa s.n.* (holotype, TI).

Stems 40–120 cm tall; branches ascending at an angle from the stem less than 45°. Cauline leaves oblanceolate or narrowly oblong, serrate, less often crenate, or rarely entire, 4.7–7(–10) × (0.7–)0.8(–

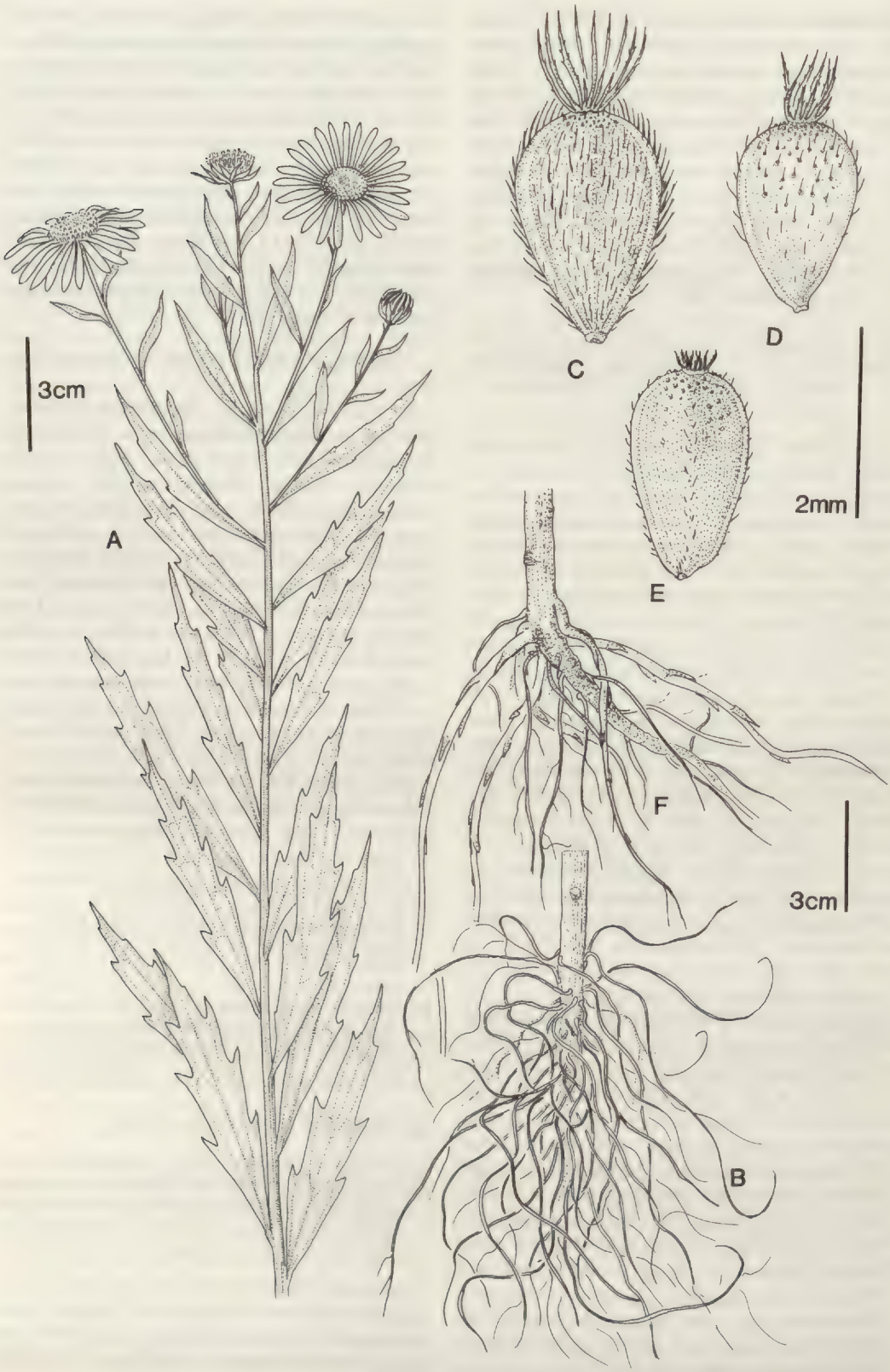

3cm
A
C
D
2mm
E
F
3cm
B

Figure 10. Geographical distribution of *Kalimeris incisa* subsp. *incisa* (dots) and subsp. *macrodon* (star, indicated by arrow).

2.2) cm, with scattered nonglandular hairs on both sides or glabrous adaxially and loosely hairy abaxially. Capitula 10–55; peduncles (1.8–)4–10(–18) cm long; bracts 3–9 along the peduncle, the lower ones 8–17(–23) × 1–1.6(–6) mm, the upper ones 2.1–5.4(–8) × 0.3–1.4(–2.5) mm; involucre hemispherical, 7–11 mm broad, 5–6.5 mm high. Phyllaries in 3 whorls, loosely imbricate; those of the outermost whorl (3.1–)3.5–5.2 × (0.7–)0.9–1.3 mm, those of the middle whorl(s) 4.2–5.8(–6.4) × 1.1–1.6(–1.9) mm, those of the inner whorl 4.9–6(–6.5) × 1–1.6(–1.8) mm. Receptacles convex or subconical, (1.4–)1.8–2.3 mm wide, (0.8–)1.2–1.8 mm high. Ray florets (13–)16–27; corollas pale lilac, ligules 15.8–22 × (1.8–)2.1–3 mm, the tube (0.8–)1–1.6 mm long; style (1.6–)1.9–2.8 mm long, the branches 0.7–1.2 mm long. Disc florets (40–)71–115; corollas 3–4(–4.2) mm long, the lobes unequal, the longer one 1–1.7(–2) mm long, the shorter ones 0.5–1.1(–1.5) mm long, both 0.3–0.6 mm wide, tube (0.6–)0.9–1.2(–1.4) mm long; anther 0.9–1.4(–1.6) mm long; style (2.1–)2.5–4(–4.3) mm long, the branches 0.8–1.3 mm long. Ray and disc pappus bristles equal or sometimes unequal; ray bristles (0.2–)0.5–1 mm long; disc bristles 0.5–1.2(–1.5) mm long. Achenes straw-colored, the margins 0.2–0.4 mm wide; ray achenes 2.6–3.1 × 1.4–1.5 mm; disc achenes 2.6–3.1 × 1.4–2.2 mm. Chromosome number: $n = 9$. Figure 9A–C.

Phenology. Flowering period: late June to October.

Distribution (Fig. 10). Amur and Ussuri basins (southern Far East region of Russia, possibly in eastern Siberia but without accurate localities) to the Daxing'anling Mountains in Heilongjiang and to Nei Mongol Zizhiqu, and through Jilin and Liaoning provinces, southward to Korea in the following provinces: Hambook, Hamnam, Pyong-Book, Hwanghe, Gyong-gi, Seoul, Choongbook, Choongnam, Gyong-nam, Boosan, and Junnam. Most populations occur from sea level to about 900 m elevation. This taxon is fairly common and grows in relatively mesic, semi-open secondary-growth forests, in meadows, and along margins of mixed coniferous and broad-leaved forests. It is rarely found along dry roadsides, where the populations are very small, sometimes comprising only one or a few individuals.

Kalimeris incisa subsp. *incisa* is often sympatric with *K. integrifolia* and *K. mongolica*, and all three have been found growing side by side with very slight habitat differentiation. Sometimes they can be found mounted together under the same collection number (e.g., *James s.n.*, May–Aug. 1886, K). Usually, *K. incisa* subsp. *incisa* grows in relatively mesic and protected areas, e.g., under trees, shrubs, or among taller herbs, whereas *K. integrifolia* and *K. mongolica* occur in drier and more exposed places. It seems that *K. incisa* subsp. *incisa* and *K. integrifolia* do not hybridize with each other, because no intermediates have been found in areas of overlap. Intermediates between *K. incisa* subsp. *incisa* and *K. mongolica* (e.g., *Kitamura s.n.*, 15 Sep. 1939, KYO) are rarely found in the areas where populations of the two taxa occur together.

This subspecies tends to grow more vigorously in the northern part of its distributional range. Individuals in the Amur basin are more robust than those in the southern part of the range. Based on this observation, Kitagawa (1936) gave varietal sta-

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Figure 9. *Kalimeris incisa* and *K. pinnatifida*. A–C. *K. incisa* subsp. *incisa*. —A. Upper branch. —B. Root. —C. Achene. —D. Achene of *K. incisa* subsp. *macrodon*. E, F. *K. pinnatifida*. —E. Achene. —F. Root and elongated rhizomes.

tus to the southern populations, as *Kalimeris incisa* var. *australis*. Kitamura also annotated herbarium specimens from Tumenling, China, as "*Kalimeris tatewakiana*," and noted on one of the labels that the plants were smaller than typical *K. incisa* and were cultivated at Kyoto University for further studies. It seems that the studies on these plants were not completed because neither the name *K. tatewakiana* nor any discussion on this subject has ever been published. There are many intermediates between these two forms, suggesting a clinal pattern, and because there are no other differences correlated with size, these extreme forms are regarded as a single taxon in the present treatment.

The leaf morphology of this subspecies is very variable. Some individuals have almost entire leaves, whereas others have deeply pinnate-lobed leaves. On Mt. Qianshan, Liaoning, China, individuals with narrowly oblanceolate and broadly oblanceolate leaves grow together in the same population (*H. Gu & W. Zhang 279, 280,* MO). The length of the pappus bristles tends to be reduced in populations at the southern part of the geographic range, especially in South Korea. Generally, Korean plants tend to have shorter pappus bristles and more slender branches than those found on the continent.

Several specimens (e.g., *Horsfield 788,* K, BM) from Java with Miquel's annotation "*Aster indicus* β *horsfieldii*" belong to *K. incisa* subsp. *incisa,* and were most likely cultivated there. In any case, *Aster indicus* β *horsfieldii* was never published. One specimen, *W. Souder 253* (BM) from "Rochester, North America," is either mislabeled (as noted on the sheet) or was collected from cultivated plants, since there are otherwise no collections known from North America.

Additional specimens examined. RUSSIA. **Amur:** Blagoveschensk, *Karo 182* (BM, E, K, G, P). **Primorski:** Vladivostok, *Saberkin 613* (NY), *770* (NY). **Siberia:** *Faughe s.n.* (G), *Gadleeau 3944* (BM), *Jacq s.n.* (K), *Klatt s.n.* (GH), *Turczaninow s.n.* (P); "Dahuria," *Fischer 17* (G), *Turczaninow s.n.* (GH); "Amur River," *Maximowicz s.n.* (G, GH, K, NY). KOREA. **Hambook:** Kyongsong, *Saito 1568* (KYO). **Hamnam:** Hamhung, Katokori, *Nomura 53* (KYO); Hesan, Jindebo, *Nakai 2773* (TI); Samsu, *Nakai 3592* (TI); Togwon, *Kitamura s.n.* (KYO, TNS); Wosan, *Kitamura s.n.* (KYO). **Pyong-Book:** Gangge, *Mills 136* (TI), *145* (TI), *410* (TI); Yongsandong, *Nakai 2785* (TI). **Hwanghe:** Mt. Jangsoo, *Koidzumi s.n.* (KYO). **Gyong-Gi:** Suwon, *Sakata 498* (KYO). **Seoul:** Changduk Palace, *Okada s.n.* (TI); Mt. Bookhan, *Uchiyama s.n.* (TI); Gwangrung, *Lee et al. 6826* (TI), *Nakai 13218* (TI); Mangwoori, Seoul, *Chung 9288* (TNS); Mt. Nam, *Faurie 393* (KYO, P), *403* (KYO), *404* (P), *Okada s.n.* (TI); Seoul, *Dann 54* (BM), *Bodinier s.n.* (E). **Choongbook:** Chungju City, *Lee et al. 6627* (TI). **Choongnam:** Gongjoo-goon, Geryongmyon, *Kashimura s.n.* (KYO). **Gyong-Nam:** Chinju, *Uno 22976a* (GH); Mt. Jili, *Okamoto 16067* (KYO), *16068* (MAK). **Boosan:** Dongre, *Kitamura s.n.* (KYO). **Junnam:** Kwangju, Mt. Kwang, *Chung 473* (TNS), *3107* (KYO, TNS). CHINA. **"Manchuria":** Amur River, Mt. Burejae, *Radde 86* (P); "Chara," *Komarov 1507* (BM, P); Xing'an Mts., Dzhalantun, *Litvinov 2556* (NY), *Karo 1507* (K, P). **Heilongjiang:** Acheng Xian, Yichuomao-shan, Baimaozi, *G. Wang 498* (IFP); Boli Xian, Hongqi Forestry Station, *Y. Zhang et al. 2117* (IFP); Mao'ershan Xian, Xingshi, *G. Wang & Q. Li 26* (IFP); Mishan Xian, Hulin, *Heilongjiang Expedition Team 142* (IFP), *151* (IFP), *205* (IFP); Ning'an Xian, Shihuan-zheng, Nanhutou, *Y. Zhang et al. 1226* (IFP); Suiling Xian, Ruisui-cun, *Maguro s.n.* (KYO); Sunwu Xian, Siji-dun, *G. Cui & C. Lin 1483* (IFP), *1499* (IFP); Yanxing Xian, from Luobei to Xingdongcun, *C. S. Wang 128* (IFP), *172* (IFP). **Nei Mongol:** Bugt, *Kitagawa s.n.* (TI); Ningcheng Xian, Cunjingou-gongshe, Songshuling, 200 m, *S. Li et al. 4655* (IFP); Solon Qi, Honggoli, *S. Liu et al. 8298* (IFP, PE); Xing'anling Mts., *Ishidoya s.n.* (KYO). **Jilin:** Antu Xian, 285 m, *S. Liu 3685* (IFP, PE); Changbai-shan, Huapihe, 900 m, *S. Liu et al. 1802* (IFP, PE); from Changbai-shan to Tanghoko, *James s.n.* (GH, K); Fusong Xian, Donggang, 780 m, *S. Liu et al. 1282* (IFP, PE), *1363* (IFP, PE); Helong Xian, Huanchengxiang, Qingshan, *T. Wang 2465* (IFP), *2572a* (IFP); from Huapihe to Manjiang, 900 m, *Y. Zhang & S. Wang 657* (IFP); Hunchun Xian, Chunhua-xiang, Lanjiatangzi, *T. Wang et al. 2182* (IFP); Jilin Shi, Longtan-shan, *Kitagawa s.n.* (TI); Xiaobai-shan, *P. Fu et al. 2180* (IFP); Jiaohe Xian, Shuangshanto, Banggengdingzi, *Y. Chou et al. 2259* (IFP); Jiutai Xian, Tumenling, *Yamatsuta 99* (TNS), *K. Chou 2128* (IFP); Linjiang Xian, Yalujiang River, *Y. Li et al. 821* (IFP, KUN, PE); Manjiang Xian, Changbai-shan, 900 m, *J. Qian 850* (KUN), *955* (KUN); Tanghoko, *James s.n.* (K); Wuihulin, Ma'an Shan, *Kitagawa s.n.* (TI); Xing'anling Mts., *Yamatsuta 87* (TNS), *93* (TNS); Zhangjiadian, *T. Wang 1671* (IFP). **Liaoning:** Anshan Shi, Qian-shan, *H. Gu & W. Zhang 276* (MO), *279* (MO), *280* (MO); Changbai-shan, Yuheng-shan, *S. Li 760* (IFP); Shenyang Shi, Donglin, *H. Gu et al. 266a* (MO), *270* (MO).

1b. Kalimeris incisa subsp. **macrodon** (Vaniot & H. Lév.) H. Y. Gu, stat. et comb. nov. *Aster macrodon* Vaniot & H. Lév., Bull. Acad. Int. Géogr. Bot. 20: 141. 1909. TYPE: Korea. Cheju Island (Quelpart), 25 Sep. 1906, *Faurie 1071* (holotype, E; isotypes, BM, KYO).

Stem 30–52 cm tall; branches ascending at an angle from the stem greater than 45°. Cauline leaves obovate to elliptical, crenate or less often deeply serrate, 2.6–7.6 × 1–3.4 cm, glabrous or with scattered nonglandular hairs adaxially. Capitula (15–)19–29; peduncles (2.8–)3.8–8.6 cm long, bracts 2–5 along the peduncle, the lower ones 9–12(–20) × 2.5–5.5 mm, the upper ones 4.7–7.5 × 1–1.8 mm; involucre hemispherical, rarely campanulate, (7–)8.5–10 mm broad, 5–6 mm high. Phyllaries in 3–4 whorls, imbricate; those of the outermost whorl 3.2–4.5(–4.8) × 0.9–1.3 mm, those of the middle whorl(s) (4–)4.5–6 × 1–2 mm, those of the inner whorl 4.7–6.5 × 1.6–2.2 mm. Receptacles subconical, (1.1–)1.5–2.4 mm wide,

(1.2–)1.6–2.1 mm high. Ray florets 19–29; corollas pale lilac to pale purple, ligules 8.6–15.5(–16) × 2.2–3.2 mm, the corolla tube (1.1–)1.5 mm long; style (1.5–)1.9–2.8 mm long, the branches 0.7–1.2 mm long. Disc florets (58–)68–112; corollas 3.3–4 mm long; the lobes unequal, the longer one 1.1–1.8 mm long, the shorter ones 0.8–1.4 mm long, both 0.5–0.6 mm wide, the tube 0.9–1.1 mm long; anther 1–1.4 mm long; style 2.2–2.9 mm long, the branches 0.9–1.3 mm long. Ray and disc pappus bristles often brownish, unequal; ray bristles 0.2–0.6 mm long; disc bristles 0.4–1 mm long. Achenes straw-colored or greenish, the margins 0.1–0.3 mm broad; ray achenes 2–2.8 × 1.3–1.5 mm; disc achenes 2.2–3 × 1.5–1.9 mm. Chromosome number unknown. Figure 9D.

Phenology. Flowering period: July to October.

Distribution (Fig. 10). This subspecies is endemic to Cheju Island, South Korea, the southern limit of *Kalimeris incisa*, where it is sympatric with *K. indica* subsp. *indica*. It occurs apparently from near sea level to 800 m.

This taxon may hybridize with *Kalimeris indica* subsp. *indica*, as evidenced by some individuals of *K. incisa* subsp. *macrodon* with shorter pappus bristles.

Additional specimens examined. KOREA. **Cheju Island:** 800 m, *Taquet 950* (G), *951* (G, TNS), *952* (G), *990* (E, K), *991* (E, TNS), *992* (TNS); "Hoabin," *6236* (TI); South Cheju, *Nakai 6519* (TI); North Cheju, *6522* (TI).

2. Kalimeris pinnatifida (Maxim. ex Makino) Kitam., Acta Phytotax. Geobot. 6: 50. 1937. *Aster indicus* var. *pinnatifidus* Maxim. ex Makino, Bot. Mag. (Tokyo) 20: 41. 1906 ["*pinnatifida*"]. *Aster pinnatifidus* (Maxim. ex Makino) Makino, in Iinuma, Somoku-Dzusetsu 4: 1106. 1912. *Aster incisus* var. *pinnatifidus* (Maxim. ex Makino) Nakai, Bot. Mag. (Tokyo) 33: 215. 1919. *Asteromoea pinnatifida* (Maxim. ex Makino) Koidz., Bot. Mag. (Tokyo) 37: 56. 1923. TYPE: Japan. Kanagawa: Yokohama, *C. J. Maximowicz s.n. in 1862* (holotype, LE not seen; isotypes, BM, GH, W).

Aster indicus f. *hortensis* Makino, Bot. Mag. (Tokyo) 20: 41. 1906 ["*pinnatifida*"]. *Asteromoea indica* f. *hortensis* (Makino) Matsum., Index pl. jap. 2(2): 609. 1912. *Aster pinnatifidus* var. *hortensis* (Makino) Makino, in Iinuma, Somoku-Dzusetsu 4: 976. 1913. *Kalimeris pinnatifida* var. *hortensis* (Makino) Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 13: 309. 1937. TYPE: Japan. Kochi: Takaodo-gun, Sakawa-cho, 28 June 1887, *T. Makino s.n.* (lectotype, here designated, MAK).

Aster pinnatifidus f. *albescens* Makino, J. Jap. Bot. 7: 10. 1931. *Kalimeris pinnatifida* f. *albescens* (Makino) Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 13: 309. 1937. TYPE: Japan. Iwate: Morioka, *T. Makino s.n., s.d.* (holotype, MAK).

Aster pinnatifidus f. *caeruleus* Makino, J. Jap. Bot. 7: 10. 1931. *Kalimeris pinnatifida* f. *caerulescens* (Makino) Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 22: 309. 1937. TYPE: Japan. Fukushima: Yatakawa-mura, *S. Nemoto s.n., s.d.* (holotype, MAK).

Root fibrous; rhizomes stoloniferous, 15–20 cm long. Stem 56–130 cm tall. Cauline leaves oblong to oblanceolate or less often broadly oblanceolate, serrate to deeply pinnate-lobed, (3.4–)5–8(–10.5) × (0.4–)1–2.5(–3.4) cm, glabrous or with scattered nonglandular hairs adaxially, loosely or sometimes densely covered with nonglandular hairs and with scattered glandular hairs abaxially, lobes lanceolate to triangular, 0.2–0.9 × 0.1–0.5 cm. Capitula 20–88; peduncles (1–)2–8.5(–16) cm long; bracts 2–6(–10) along the peduncle, the lower ones 10–25 × 1.5–5 mm, the upper ones 2.5–7.8 × 0.5–1.2 mm; involucre hemispherical or rarely campanulate, 7–10 mm broad, (3.5–)4.2–5.5(–6.5) mm high. Phyllaries in 3–4 whorls, loosely imbricate; those of the outermost whorl (2.1–)3–4.5(–5.1) × (0.6–)0.9–1.4(–1.9) mm, those of the middle whorl(s) oblanceolate, oblong, or less often spathulate, (3.2–)3.5–5.6(–6.1) × 1–1.8(–2.2) mm, those of the inner whorl oblanceolate, oblong, or spathulate, 4–5.6 × 1–1.8(–2) mm. Receptacles convex to subconical, alveolate, 1.1–1.8(–2.2) × 0.8–1.3 mm. Ray florets (10–)14–23; corollas pale lilac to whitish, ligules 10–17 × 1.6–3.5 mm, the tube 0.7–1.4 mm long, style 1.5–2.1(–2.6) mm long, the branches 0.6–1.2 mm long. Disc florets (35–)46–71(–85); corollas 2.8–3.8(–4) mm long, the lobes equal or subequal, 0.8–1.5 × 0.4–0.6 mm, the tube 0.7–1.2(–1.4) mm long; anther 0.8–1.3(–2) mm long; style 2.2–3.3 mm long, the two style branches 0.8–1.2 mm long, each with a triangular appendage 0.3–0.5 mm long. Ray and disc pappus bristles similar, whitish, 0.2–0.3 mm long. Achenes straw-colored to purplish, obovate to broadly obovate, covered with biseriate hairs and glandular hairs at the top, the margins about 0.1–0.2 mm broad; ray achenes 3-ribbed, 2–2.6 × 0.8–1.5 mm; disc achenes 2-ribbed, 2.1–3 × 1.2–2 mm. Chromosome number: $n = 9$. Figure 9E, F.

Phenology. Flowering period: June to October.

Distribution (Fig. 11). Endemic to Japan, where it ranges from southern Hokkaido to northern Kinki Districts. It is probably not very common in Hokkaido, because only a few specimens have come from there. *Kalimeris pinnatifida* is common in Honshu, usually occurring in disturbed and rela-

Figure 11. Geographical distribution of *Kalimeris pinnatifida*.

tively mesic habitats. This species ranges from sea level to 1700 m elevation.

The epithet *pinnatifida* was first used by Maximowicz in an annotation as "*Boltonia indica* β *pinnatifida*." This name was not validated until Makino published the combination *Aster indicus* var. *pinnatifidus* in 1906. Prior to that, Matsumura had published *Asteromoea indica* var. *pinnatifida*, and *Boltonia indica* var. *pinnatifida* in 1886 and 1895, respectively, but did not provide a description or diagnosis in either case. According to Article 32.1 of the *International Code of Botanical Nomenclature*, these names were not validly published by Matsumura.

Morphologically, *Kalimeris pinnatifida* is most similar to *K. incisa*, and, like it, also grows robustly in the northern part of its distributional range. However, its short pappus bristles, stoloniferous rhizomes, equal corolla lobes, and glandular achenes make it distinct from *K. incisa* (Fig. 9).

Populations of this species are generally not very big; the only known exception is a large population (about 200 m²) at Sakyo-ku, Kyoto, in an abandoned paddy field. This species has probably been cultivated for a long time in Japan and other countries. Some selected strains have tubular disc florets of the same length as the ray florets, whereas others have long, tubular ray florets. Makino's *Kalimeris pinnatifida* var. *hortensis* was based on such a cultivated plant. Specimens with similar characteristics have been collected from cultivation in Nagasaki, Kumamoto, Tokyo, and Hyogo. *Kalimeris pinnatifida* has also been introduced into the United States; a specimen from Durham County, North Carolina (*Wood s.n. in 10/1956*, GH), clearly belongs here. Another collection from the Missouri Botanical Garden (*Kellogg s.n. in 6/1911*, MO), originally determined as *Aster incisus*, also represents *K. pinnatifida*.

Additional specimens examined. JAPAN. **Hokkaido:** Asahikawa-shi, Ishikari, *Arai s.n.* (TNS). **Aomori:** Aomori-shi, Aomori, *Faurie 1014* (MO), *5158* (W); Hachinohe-shi, 6 km W of Hachinohe Station, *H. Gu & Yahara 315* (MO); from Shirahama to Ashigesaki, *H. Gu & Yahara 330* (MO), *Kitamura s.n.* (KYO); Kamikita-gun, Towadako-cho, 2 km S of Yachionsen to Shirenhashi, *H. Gu & Yahara 326* (MO), *326a* (MO); Kazuno-shi, 5 km S of Towada Lake, 380 m, *H. Gu & Yahara 327* (MO); Tokera, 400 m, *H. Gu & Yahara 328* (MO); Kitatsugaru-gun, Tateoka-cho, Hirataki-numa, *Furuse 27* (KYO); Kuji-shi, Ohkawame, *Murata & Tabata 49* (KYO); Mutsu-shi, Mt. Osore, 300 m, along Futamatazawa, *Murata & Koyama 41306* (KYO); Natsudomari Peninsula, Asamushi, Natsudomarisaki, *Koyama 220* (KYO); Nishitsugaru-gun, Tateoku-cho, Hiratakimura, *Furuse s.n.* (KYO); Shimokita-gun, Saimura, Harada, *Mori 53* (KYO, MAK); Shimokita Peninsula, Higashidorimura, *Furuse s.n.* (MAK); from Imotomura to Horobe, *Furuse s.n.* (A); from Tanabu to Mt. Osore, *Koyama 775* (KYO); Towada-shi, Kawajuri, 7 km SW of Maita, *H. Gu & Yahara 323* (MO); Maita, 2.4 km E of Tanehara, *322* (MO); Maita, *Mizushima & Narita s.n.* (TI), *Narita s.n.* (TI); 15 km SE of Tashirodaira, 300 m, *H. Gu & Yahara 325* (MO), *Faurie 5159* (KYO), *Kinashi s.n.* (TI). **Iwate:** Asagi-shi, Morioka, *Kikuchi s.n.* (TNS); Higashiiwai-gun, Mt. Tabashineyama, *Kikuchi s.n.* (TNS); Ichinoseki-shi, Toyoryu Shrine, *Makino 28* (MAK); Iwategun, Iwate Mts., from Daijigoku to Yashikidai, *Koyama 1492* (KYO, TNS); Isawa-gun, Isawa-cho, SE of Mt. Yakeishidake, 300–500 m, *Kurosaki 11365* (KYO); Mizusawashi, Shoho-ji, Mt. Horai-san, *Makino s.n.* (MAK), *Iwabuchi s.n.* (KYO, TNS); Morioka-shi, *Makino s.n.* (MAK), *Yamada s.n.* (MAK); Noshiro-shi, Hiyama, *Hemmi 355* (KYO, MAK). **Akita:** Akita-shi, *Yamatsuta 13* (TNS). **Miyagi:** Mt. Fubou-san, Namarizawa, 800 m, *Boufford & Wood 19863* (KYO, MO); Katta-gun, Shichikasyuku-cho, Mt. Fubo-dake, 600 m, *Murata 44563* (TI); Miyagi-gun, Miyagi-cho, Mt. Ushiroshirahige, *Ogura 2458* (TI); Motoyoshi-gun, Shizugawa-cho, *Naito & Otomo s.n.* (KYO); Sendai-shi, Dainohara, *Ogura s.n.* (TI); Kawauchi, Ninomaru, *Okazaki & Kanno s.n.* (TI); Kozi, *Iishiba s.n.* (MO); Tokusayama, Kakuda, *Sugaya et al. s.n.* (MO), *Faurie 6743* (P). **Yamagata:** Akumi-gun, Yawata-cho, Kannonji, *Sato s.n.* (MAK); Higashine-shi, Takasaki-mura, *Okayama s.n.* (TNS); Higashitagawa-gun, Yamato-mura, Tsutsumishinden, *Kato s.n.* (MAK); Higashokitama-gun, Takahata-cho, Yashiromura, *Koidzumi s.n.* (KYO); Yuza-

cho, Mt. Chokai, Kannonmori, 600 m, *Ohashi s.n.* (TI); Mogami-gun, Mamurogawa-cho, Okachitoge, 400 m, *Takahashi 2838* (KYO); Takasakamura, *Nagasawa s.n.* (TNS); Murayama-shi, Ohmaki, *Takahashi 102* (MO); Tateyama, *Inoe s.n.* (MAK); Yamatata-shi, Kabutoiwa, Yamadera, *Ohba 718022* (MO, TI); Kaminoyama, *Beattie & Kurihara 11119* (GH); Yonezawa-shi, Narushima, *Midorikawa 1368* (TI). **Fukushima:** Kitakata-shi, *Makino 2* (MAK); Minamiaizu-gun, Tadami-cho, Asakusadake Mts., *Yamasaki s.n.* (TI); Tajima-cho, from Hariu to Akobara, 700 m, *Murata 9908* (TI); Hinoemata-mura, *Nasegawa s.n.* (TI); Nishishirakawa-gun, Shirakawakogen, 900 m, *Koyama 407* (A, KYO, NY); Yama-gun, Inowashiru-cho, *Akaii et al. s.n.* (TI); from Niichyuraonsen to Hinosawa, *Kurosawa s.n.* (TI); Shirakawa-shi, Yatsutakawa, *Ueno s.n.* (TNS); Tamura-gun, Miharu-cho, *Makino s.n.* (MAK). **Ibaraki:** Hitachi-shi, Nakachito, *Sato s.n.* (KYO). **Tochigi:** Asogun, Kuzuu-cho, *Tagawa & Iwatsuki 1991* (KYO); Imaichi-shi, Fubasami, 300 m, *Ohashi & Murata s.n.* (KYO, TI); Kanuma-shi, Itaga, 200 m, *Ohashi et al. 1546a* (TI); Kuruizo-shi, Ikuyohashi, *Hara s.n.* (TI); Nasu-gun, Kurobane-cho, Miyujintoge, 376 m, *Hara s.n.* (TI); Yamizo Mts., Ungan-ji, *Hara & Kurosawa s.n.* (TI); Nasuno-gun, Nishinasuno-cho, *Suzuki s.n.* (KYO); Nikko-shi, Ganmangafuchi to Mt. Nakimushi, *Takenaka 198* (TI); 700 m, *203* (TI); Mt. Nakimushi, *Ito 9* (TI); Nikko Botanical Garden, *Uehara s.n.* (TI); Shimano, *Makino s.n.* (KYO, MAK); Shimotsuga-gun, Kinagawa-mura, *Furuse s.n.* (A). **Gunma:** Numata-shi, Shidamura, *Makino 149* (MAK); Tano-gun, Ueno-mura, Fujidou, 750–900 m, *Murata et al. 6257* (KYO); Tone-gun, Mt. Mitsumine-san, *Tobe s.n.* (TNS); Usui-gun, Matsuida-cho, Mt. Myugisan, Hakuunzan, 700 m, *Murata 27445* (KYO); from Usuitoge to Yokokawa, 550 m, *H. Gu & Yahara 426* (MO). **Chiba:** Abiko-sh, *Murata & Togashi 39* (KYO, MAK); Awa-gun, Amatsukominata-cho, Kiyosumiyama, *Tashiro s.n.* (TNS); Higashikatsushika-gun, from Takayanagi to Shinden, *Kurihara et al. 160* (TI); Ichikawa-shi, *Yamamoto s.n.* (TI); Kashiwa-shi, Kitakogana, *Shirai s.n.* (TNS). **Saitama:** Chichibu-shi, Mt. Bukou, *Moriya s.n.* (TNS), *Tagawa s.n.* (KYO); Ohnomura, Ohnotoge, 850 m, *H. Gu & Yahara 427* (MO), *429* (MO), *430* (MO), 500 m, *428* (MO); Hannou-shi, Shirako, *Makino s.n.* (MAK); Naguri River, Hannou-shi, *Sugiyama s.n.* (TI). **Tokyo:** Aomei-shi, Mt. Mitakesan, 900 m, *Murata 6075* (TI); Arakawa-ku, Dakan-yama, *Makino s.n.* (MAK); Bunkyo-ku, Koishikawa Botanical Garden, *Abe s.n.* (TI); Edogawa-ku, Koiwamura, *Makino s.n.* (MAK); Fuchyu-shi, *Mizushima s.n.* (MO, TI); Hachiouji-shi, Kaminukugitahen, *Makino s.n.* (MAK); Mt. Takaosan, *Sato s.n.* (TI); Itabashi-ku, Kamiitabashi, *Makino & Kitamura s.n.* (KYO); Itsukaichi-shi, *Kobayashi 4294* (MAK); Mitaka-shi, Inokami, *Makino s.n.* (MAK); Osawa, *Elliott 144* (A); Nakanoku, *Makino s.n.* (MAK); Nelima-ku, *Makino s.n.* (MAK); Nishitama-gun, Hinohara-mura, Sengennoe, 500–900 m, *Murata 13430* (KYO); Motohachiwooj-mura, Shiroyama, *Furuse s.n.* (A); Mt. Sogakuzan, *Mizushima 12032* (MAK, cultivated); Shibuya-ku, *Makino s.n.* (KYO); Shimura, *Okuyama s.n.* (TNS); Suginami-ku, *Maekawa 160 A32* (TI); Kugayama, *Yamatsuta 4050* (TNS). **Kanagawa:** Kamakura-shi, from Yukinoshita to Juunisou, *Kobayashi 3485* (MAK), *Asai s.n.* (TI); Kamato-shi, from Atsugi-shi to Yokohama-shi, *Yamasaki s.n.* (TI); Kawasaki-shi, Noborito, SW of Tokyo, *Makino s.n.* (KYO, MAK); "Kinugasa," *Suzuki s.n.* (A); Odawara-shi, *Kankatai s.n.* (MAK); Uranoguchi, *Makino s.n.* (MAK); Tsukui-gun, Tanzawa Mts., Mt. Yake-yama, *Yamasaki s.n.* (TI); Yokohama-shi, *Hisanchi s.n.* (KYO); Zushi-shi, Numakan, *Momiyama 18* (MAK). **Niigata:** Arai-shi, Mt. Kazano, from Kamihiramaru to Nagasawa, 500–700 m, *Kurosaki 11432* (KYO); Higashikanbara-gun, Kanose-cho, *Nakai & Maruyama s.n.* (TNS); Kitakanbara-gun, Sasakami-mura, Deyuonsen, *Yatabe s.n.* (TI); Kitauwonuma-gun, Irihirose-mura, from Kobirawa to Sodeyama, *Furuse s.n.* (A); Minamiuonumagun, Muika-cho, Hakkatoge, *Kanai 6481* (A, TI); Nishikanbara-gun, Yahiko-mura, *Noda s.n.* (TNS); Ojiya-shi, *Yamasaki 8986* (TI); Sado Island: Hamochi-cho, *Ito s.n.* (TNS). **Toyama:** Kaminikawa-gun, Ohyama-cho, Kamegai, *Kurosaki 12069* (KYO); Naganiikawa-gun, Kamiichicho, Hinoya to Oiwa, *2116* (KYO); Osawa, *2298* (KYO); Toyama-gun, 17 km SW of Toyama-shi, *Kirino 386* (MO); Uotsu-shi, Katakaigawa, *Nagai s.n.* (KYO); Tsubono, 300 m, *Nagai s.n.* (TI). **Nagano:** Chiisagata-gun, Sanada-cho, Sugadaira, *Kobayashi 13126* (KYO); Toubu-cho, from Narahara to Mt. Yunomaru, 1200 m, *Murata 27540* (KYO); Chino-shi, Kirigemine, *Makino s.n.* (MAK), *Okamoto s.n.* (KYO); Hanishina-gun, Sakaki-cho, *Makino s.n.* (MAK); Iida-shi, Chiyo-mura, Yonegawa, *Koidzumi 94955* (TNS); Iiyama-shi, Mizuhokuni, *Yokouchi s.n.* (MAK); Kigashichikuma-gun, "Katooka," *Kubota s.n.* (KYO); Kamiminochi-gun, Shinano-cho, Lake Nojiriko, 700 m, *Midorikawa 1028* (TI); Togakushi-mura, Koshimizuhara, 1250 m, *2002* (TI); Kiso-gun, Kisofukushima-cho, Mitakemura, *Kawasaki s.n.* (MAK); Mt. Togakushi, Nenbutsuike, *Naruhashi 1856* (KYO); Kitaadzumi-gun, Kitoshiro-mura, *Furuse 13944* (KYO); Kitasaku-gun, Karuizawa, *Fox s.n.* (BM); Shinanooiwake, Karishuka, 1000 m, *Kanai 419* (TI); Togemashi, *Shirai s.n.* (TNS); Minamisaku-gun, Kawakamimura, Mt. Mikuniyama, Azusayama, *Kitagawa 1535* (KYO), *Murata 11818* (KYO); from Senjagahara to Mt. Mikuniyama, 1700 m, *Hotta 10181* (KYO); Koumi-cho, Mt. Yatsugatake, *Murata & Ohba 5382* (TI); Nishichikuma-gun, Kaida-mura, Nishino, 1200 m, *Nitta & Mabuchi 12012* (KYO); Nishichikuma-gun, Tadachi-mura, *Shinota 5386* (GH); Shimoina-gun, Bunkuitoge, 1250 m, *Koyama 7311* (KYO); from Kamazawa to Koshibuyu, 500–700 m, *Iwatsuki & Koyama 37* (KYO, MAK, TNS); Ooshika-mura, from Ohgawara to Momonodaira, *Murata & Shimizu 1472* (MO); Suwa-shi, Mt. Moriyasan, 1100–1650 m, *Midorikawa 508* (TI), *540a* (TI), *540b* (TI), *661* (TI); Ueda-shi, Beshuonsen, *Kitagawa 5361* (KYO); Yamakuchi-mura, Aono, *Okuhara s.n.* (KYO). **Shizuoka:** Fujinomiya-shi, Mt. Fuji, 1200 m, *Mimoro et al. 1162* (MO); Ibara-gun, Fujigawa-cho, Iwabuchi-eki, *Ohmura s.n.* (KYO); E of Mt. Kenashiyama, Fumoto, 800 m, *Hino et al. 62* (KYO); Goteba-shi, Higashitanaka, E of Mt. Fuji, 450 m, *Murata 1610* (KYO); Sunto-gun, Nagaizumi-cho, Suijinja, Mt. Ashitaka, *Fujimura & Fukui 29* (KYO); Susono-shi, S of Mt. Fuji, 900 m, *Konta 11564* (KYO). **Yamanashi:** Higashiyamanash-gun, Santomi-mura, Mt. Kentokusan, 1600–1700 m, *Midorikawa 1729* (TI); Kitakoma-gun, Hakushiyu-cho, Mt. Koma, *Kitamura s.n.* (KYO); Kitatsuru-gun, Uenohara-cho, Shiotsu, *Okamoto s.n.* (KYO); Tanakami, *Okamoto s.n.* (KYO); Minamikoma-gun, Nanbu-cho, Kozori, 400–700 m, *Tateishi et al. 4563* (TI); Minamishuru-gun, Nishikashura-cho, Mt. Mitsutougeyama, *Kobayashi s.n.* (MAK, KYO); Nirasaki-shi, Mt. Houou, 700 m, *Yamasaki s.n.* (TI); Nishiyatsushiro-gun, Kamikuishiki-mura, Asagirikogen, Mt. Fuji, 900 m, *Murata et al. 33895* (A); Lake Motosu, Mt. Fuji, *Furuse s.n.* (A); Nanbu-cho, Kozori, 400–700 m, *Tateishi et al. 4363* (TI). **Aichi:** Atsumi-gun, Fukue-cho, Kameyama, *Torii s.n.* (KYO); Kitashitara-gun, Inabu-cho, Kawahe, *Torii s.n.* (KYO); Ninamishitara-gun, Tsukude-mura, between Kamogaya and Yuanami, 500 m, *Murata 13232* (KYO); Shi-

tara-cho, Nokoenhan, *Matsuoka s.n.* (MAK); Sumikawa, Mt. Dando, *Murata 6716* (KYO); Niwa-gun, Fuso-mura, *Kurachi 7926* (GH); Yana-gun, Funatsuke-mura, *Torii 2388* (KYO). **Gifu:** Gujyo-gun, Takasu-mura, Hirugano, 890 m, *Murata 14351* (KYO); Gushiyou-gun, Shirutori-cho, Nagataki, *Shiota 689* (GH); Ohno-gun, Kuguno-cho, from Dangumi to Mt. Funayama, *Fukuoka 7518* (KYO, TNS); Yoshiki-gun, Kamitakara-mura, Miyahara, *Tomioku 5972* (GH). **Ishikawa:** Mt. Iosen, *Murakami s.n.* (MAK), *Tanaka s.n.* (MAK); Kashima-gun, Kashima-cho, Sekidozan, 400 m, *Yamasaki s.n.* (TI); Suzu-shi, Suzuzinzya, Mt. Yamabusiyama, *Masamune 14176* (KYO). **Fukui:** Minamirokuro-shi, Karasawa, 500–800 m, *Kurosaki 11104* (KYO); Nanjo-gun, Imajo-cho, Shinbo, Kinometoge, Hiyoshi Shrine, *Kanai 731271* (TNS); Ohno-shi, from Fukai to Mt. Iifuriyama, *Fukuoka 8265* (KYO); Mt. Kyogatake, *Murata & Shimizu 329* (KYO); Takefu-shi, Ohshio, 60–160 m, *Kurosake 8019* (KYO, TI); Tsuruga-shi, Ikenokochi, 250 m, *Kitamura & Murata 2079* (KYO). **Shiga:** Takashima-gun, Kawakami-mura, *Hashimato 4670* (TNS); Kuchiki-mura, Udoya, Inumaru, 300 m, *Kurosaki 11893* (KYO), *Ohba & Akiyama 1987* (TI). **Kyoto:** Atago-gun, Kurama, *Kitamura s.n.* (KYO); Kitakuwada-gun, Miyama-cho, Ashu, *Okamoto s.n.* (KYO, TNS); Kyoto-shi, Sakyo-ku, Hirogawara, 40–60 m, *H. Gu et al. 415* (MO); between Kibune and Hanasetoge, *Tagawa 106* (KYO); Nomi, N of Hanase, 600 m, *Murata 17491* (KYO, US); Kuta, 60–100 m, *H. Gu et al. 414* (MO); between Kuta and Hirogawa, *Hiroe 16362* (KYO, TI); Sisigatani, *Tagawa 2989* (MAK, NY), *Stowe s.n.* (TI).

3. Kalimeris mongolica (Franch.) Kitam., Acta Phytotax. Geobot. 6: 21. 1937. *Aster mongolicus* Franch., Nouv. Arch. Mus. Hist. Nat. 6: 41. 1883. *Aster lautureanus* var. *mongolicus* (Franch.) Kitag., Bot. Mag. (Tokyo) 48: 110. 1934. *Asteromoea mongolica* (Franch.) Kitam., Acta Phytotax. Geobot. 4: 21. 1937. *Kalimeris lautureana* var. *mongolica* (Franch.) Kitag., Neo-lin. fl. manshur. 653. 1979. TYPE: China. Hebei: Chengde (Mongolie: Géhol), July 1864, *A. David 1995* (lectotype, here designated, P; isolectotype, P).

Kalimeris incisa var. *holophylla* Maxim., Prim. fl. amur. 146. 1856. *Aster lautureanus* var. *holophyllus* (Maxim.) F. H. Chen, Bull. Fan Mem. Inst. Biol. 5: 41. 1934. TYPE: Amur: Aug. 1856, *Maximowicz s.n.* (holotype, LE not seen; isotypes, BM, G, K, P).

Aster associatus Kitag., Rep. Inst. Soc. Res. Manchoukuo 2: 229. 1938. *Kalimeris associata* (Kitag.) Kitag., Neo-lin. fl. manshur. 652. 1979. TYPE: China. Heilongjiang: Ke-shan, 12 Sep. 1937, *M. Kitagawa s.n.* (holotype, TI; isotype, TI).

Aster associatus var. *stenolobus* Kitag., Lin. fl. manshur. 435. 1939. *Kalimeris associata* f. *stenoloba* (Kitag.) Kitag., Lin. fl. manshur. 435. 1939. TYPE: China. Jilin: near Xinjing Xian, 17 Aug. 1938, *M. Kitagawa s.n.* (holotype, TI).

Aster associatus f. *brachylobus* Kitag., Lin. fl. manshur. 439. 1939. *Kalimeris associata* f. *brachyloba* (Kitag.) Kitag., Lin. fl. manshur. 439. 1939. TYPE: China. Jilin: near Xinjing Xian, 17 Aug. 1938, *M. Kitagawa s.n.* (holotype, TI).

Root fibrous; rhizomes condensed, forming rootstocks up to 3 cm diam. Stem 50–122 cm tall. Cauline leaves narrowly oblong to oblanceolate, serrate to deeply pinnate-lobed, (3.5–)5–8.5(–9.6) × 0.9–2.1 cm, glabrous, less often loosely covered with nonglandular hairs on both sides or only so abaxially, lobes lanceolate to triangular, 0.5–1.5 × 0.2–0.4 cm. Capitula 12–45; peduncles 2.5–11 cm long; bracts 2–7 along the peduncle, the lower ones 9–23 × 1.4–4 mm, the upper ones 4–8 × 0.8–1.3 mm; involucre campanulate or hemispherical, 6.8–13 mm broad, 5.2–7(–8.5) mm high. Phyllaries in 3–4 whorls, imbricate, glabrous or loosely covered with nonglandular hairs, chartaceous below, blunt, sometimes purplish; those of the outermost whorl lanceolate to obovate, (2.7–)3.5–6(–7.2) × 0.8–1.8(–2.8) mm, those of the middle whorl(s) obovate to spathulate, 4.2–7(–8.1) × 1.5–3(–3.5) mm, those of the inner whorl obovate to spathulate or few innermost ones oblanceolate, 4.2–7(–8) × 1.1–2.8(–3.2) mm. Receptacles convex, 1.6–2.7 mm wide, 0.7–1.6(–2) mm high. Ray florets (11–)14–25; corollas pale lilac to lilac, ligules oblanceolate, 13.5–25.5 × 2.7–4.8(–5.2) mm, the tube 1.1–1.8(–2.1) mm long; style 2–2.8(–3.4) mm long, the branches (0.5–)0.7–1.4 mm long. Disc florets 38–86; corollas 3.5–4.9 mm long, the lobes unequal, the longer one 1.2–2.1 mm long, the shorter ones 0.8–1.7 mm long, both (0.4–)0.5–0.7(–0.8) mm wide, the tube 0.8–1.6(–1.8) mm long; anther 1–1.6(–1.8) mm long; style 3–4.2 mm long, the branches 0.9–1.5 mm long, each with a triangular appendage 0.4–0.5 mm long. Ray and disc pappus bristles brownish, unequal; the ray bristles 0.3–0.5 mm long, rarely up to 0.8–1 mm long; the disc bristles 0.5–1.2 mm long, very rarely up to 1.5 mm. Achenes straw-colored to brownish, broadly obovate, loosely covered with 4-celled nonglandular hairs, rarely scattered with biseriate glandular hairs at the top, the margins 0.3–0.6 mm broad; the ray achenes 2.8–3.2 × 2–2.2 mm; disc achenes 3.2–3.5 × 2.3–2.9 mm. Chromosome number: $n = 27, 54$. Figure 12A–F.

Phenology. Flowering period: June to October.

Distribution (Fig. 13). Reaches its northern limits in the Amur basin in the Far East region of Russia and in adjacent Heilongjiang province of China, extending south and west in China to Jilin, Liaoning, Nei Mongol, Hebei, and Beijing provinces; it also extends southeastward in Korea to Hambook, Hamnam, Pyongbook, Pyongyoung, Whanghai, Kyonggi, and Seoul provinces. This distribution is similar to that of *K. incisa* except that *K. mongolica* extends further south into Laiyuan in Hebei Prov-

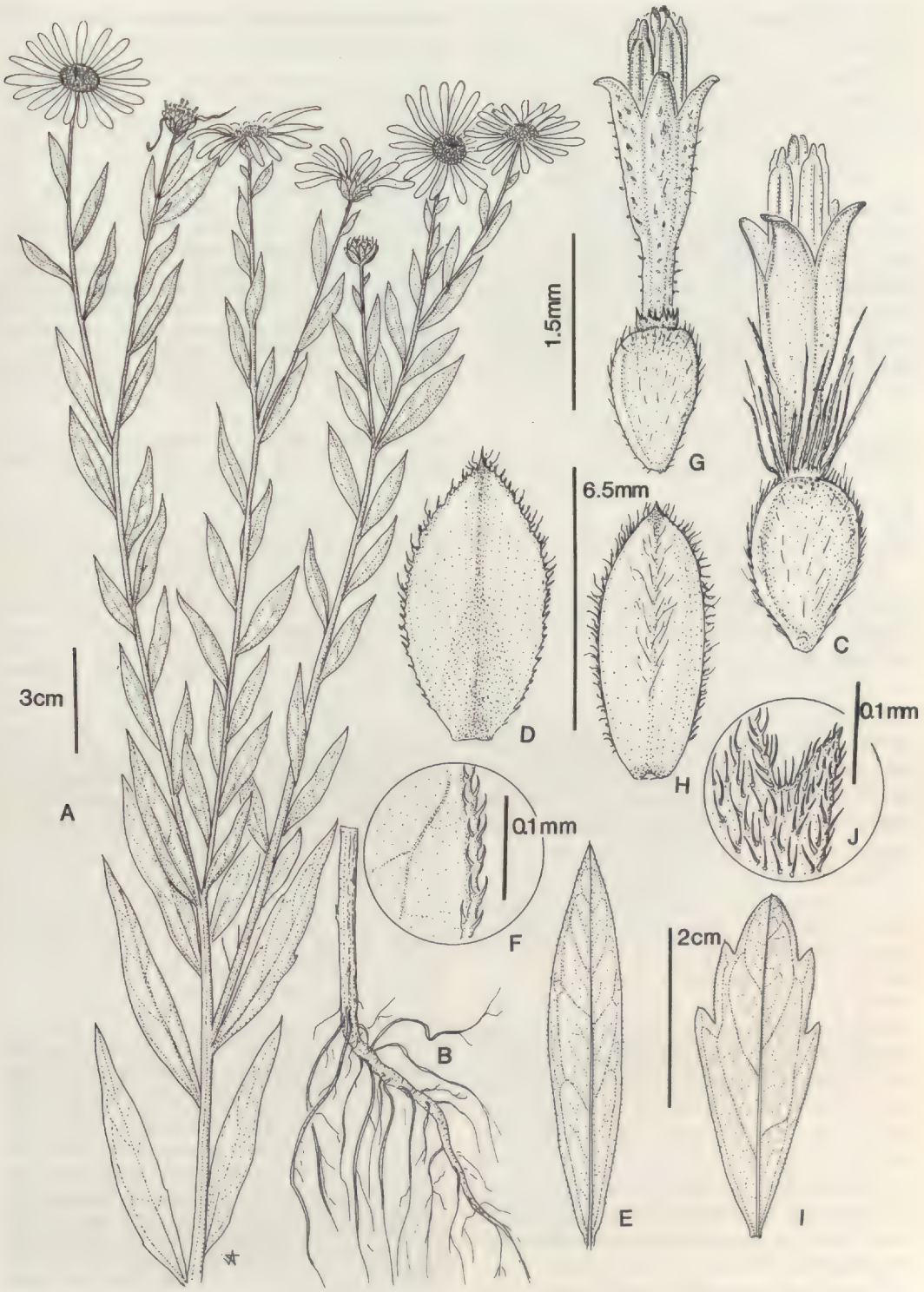

Figure 12. *Kalimeris mongolica* and *K. shimadai*. A–F. *K. mongolica*. —A. Upper branch. —B. Root. —C. Disc floret. —D. Phyllary at the middle layer. —E. Leaf. —F. Portion of the leaf showing indumentum. G–J. *K. shimadai*. —G. Disc floret. —H. Phyllary at the middle layer. —I. Leaf. —J. Portion of leaf showing indumentum.

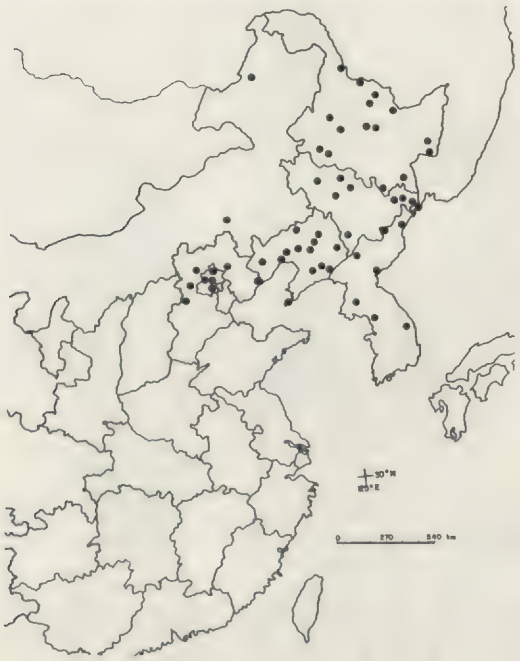

Figure 13. Geographical distribution of *Kalimeris mongolica*.

ince, China. This species grows from near sea level to 1200 m. In addition to growing in disturbed areas near human activity like most *Kalimeris* species, *K. mongolica* is commonly found in semi-open secondary forests and along edges of coniferous and mixed broad-leaf forests in relatively mesic sites.

Two specimens were designated when this species was published, i.e., *David 1995* and *2189*; the former was chosen as lectotype because it has more sheets. *Kalimeris mongolica* has been confused in the herbarium not only with *K. lautureana*, but also with *K. pinnatifida* and *K. incisa*. Handel-Mazzetti identified some Chinese *K. mongolica* as *K. pinnatifida* because of their pinnate-lobed leaves. In fact, *K. mongolica* is relatively easy to distinguish from these three species. It can be distinguished from *K. incisa* by its bigger capitula and broad phyllaries with the upper portion herbaceous and the margins broad and membranous, and from *K. lautureana* and *K. pinnatifida* by its thinner leaves, longer pappi, and broader, thickened achene margins (Fig. 9).

This species is sympatric with *Kalimeris incisa* subsp. *incisa* throughout most of its geographic range. In the field, one can observe small differences in microhabitat, however, with *K. mongolica* growing in more disturbed, open places close to roads and paths, and *K. incisa* subsp. *incisa* growing in more sheltered and natural places.

Additional specimens examined. RUSSIA. **Primorski:** Khanka Lake, *Bohnhof 41* (E, G, NY, P), *Rock 41* (NY); Ussurisk, *Schaga s.n.* (TI). **Amur:** Amur Medius, *Korshinsky s.n.* (GH). KOREA. **Hambook:** Kyongsong, *Mori 282* (TI). **Hamnam:** Mt. Changpai, *Oguma s.n.* (TNS); Hamkyong, *Okuyama s.n.* (TNS). **Pyongbook:** Gang-ge, *Mills 141* (TI). **Pyongyoung:** southern Pyongyoung, *Smith s.n.* (GH). **Whanghai:** "Sorai Beach," *Smith s.n.* (US). **Kyonggi:** Kwangnung, 37°44′ N, 128°06′ E, *Chung 3101* (TNS). **Seoul:** Mt. Nam, *Uchiyama s.n.* (KYO, TI). CHINA. **Northeast China ("Manchuria"):** *F. H. Chen 328* (NY), *Kozlow 14382* (W), *14389* (BM), *David 2029* (P). **Heilongjiang:** Daxing'anling Mts., "Chalautun," *Skvortzov s.n.* (GH); Dailing, *Takenouchi s.n.* (MAK); Harbin Shi, Guangxing-tun, *Skvortzov s.n.* (GH), *Jettmar s.n.* (W); Hailun Xian, *Kitagawa s.n.* (TI); Heli, Jinfeng-cun, *Tatewaki 31540* (KYO); Jinpohu, Diaoshuilou, *Sato 10220* (IFP, PE); Beihutou, *10219* (IFP, PE); Lanxi Xian, Tuchengzi, *Zhang et al. 1864* (PE); Luobei Xian, Luobei, *C. S. Wang et al. 72* (IFP); Mishan Xian, Hulin, *Heihuangdi Team s.n.* (IFP); Yong'an, *Asai s.n.* (KYO); from Xicangku to Lianzhu-shan, *G. Z. Wang 321* (IFP, PE); Songhua-jiang River, *Maximowicz s.n.* (GH); Weiguo, *T. N. Liu et al. 10275* (IFP); Xiaoxing'anling Mts., Tangwanghe River, *Nakao s.n.* (KYO); Xunhe, Nanzhan, Heda-tun, *G. D. Ciu & C. Q. Lin 1528* (IFP); Zhaodong Xian, from Songzhan to Dongxinsan-tun, *G. Z. Wang et al. 1018* (PE). **Jilin:** Changbei-shan, *Mori 195* (TI); Changchun Shi, Jinyuetan, *C. S. Wang 508* (IFP), *W. Wang et al. 2656* (IFP), *Takenouchi s.n.* (MAK); Chunhua, Hadamen, *C. S. Wang et al. 2367* (IFP, KUN), *2371* (IFP), *2373* (IFP), *2381* (IFP), *2386* (IFP), *2390* (IFP), *2644* (IFP); Daxing'anling Mts., Taidong, 160 m, *Jilin Teachers' College Team 788* (PE); Dunhua Xian, Dongshuai-wanzi, *G. D. Cui & C. Q. Lin 1668* (IFP, PE); Nanmenwai, *Sato 5842* (IFP, PE), *5849* (KYO); Hunchun Xian, Chunhuaxiang, Sanjiatangzi, *C. S. Wang et al. 1897* (IFP), *2138* (IFP); Jilin Shi, Longtan-shan, *Y. L. Zhang et al. 945* (IFP, PE); Xiaobai-shan, 190 m, *P. Y. Pu & Y. L. Chou 2180* (PE); Jiutai Xian, Tumenling, *Tatewaki s.n.* (KYO), *Takenouchi s.n.* (MAK); Tonghua Xian, 40 km SW of Tonghua, *P. Y. Fu & Z. H. Zhang 451* (IFP), *464* (IFP); Ji'an to Tonghua, *Takahashi 860* (TNS), *Takahashi 547* (TNS); Wangqing Xian, Chunyang-xiang, Gaoli-cun, *P. Y. Fu et al. 959* (IFP, PE), *C. S. Wang et al. 1846* (IFP, KUN), *Komarov 1507b* (GH, NY, TI), *1510* (W). **Liaoning:** Dandong Xian, Caohekou, *Sato 1188* (IFP); Fenghuang-shan, *Yamatsuta 80* (TI), *277* (TI); Huanren Xian, *C. S. Wang et al. 3820* (IFP, PE), *3830* (IFP, PE), *3855* (IFP, PE), *3868* (IFP, PE), *4231* (IFP); Hunhe, *Yamatsuta 115* (TNS); Jianchang Xian, Daheishan Forestry Station, *C. S. Wang et al. 3180* (IFP, KUN, PE); Jinzhou Shi, Hulu-dao, *C. S. Wang 3451* (IFP, KUN), *3452* (IFP), *3453* (IFP), *3524* (IFP), *W. Wang 3526* (IFP, PE); Jing Xian, Heshang-shan, *Y. Yabe s.n.* (PE); Liaoyang Xian, Emei-zhuang, *Kitamura s.n.* (KYO, MAK, TNS); Lushun Shi, Baiyu-shan, *Y. X. Liu & T. Wang 919* (IFP); Qian-shan, *H. Gu & H. Zhang 279* (MO), *283* (MO), *284* (MO), *286* (MO), *288* (MO), *Yamatsuta 105* (TNS); Shenyang Shi, Beilin, *Kitamura s.n.* (KYO, MAK, TI), *Yabe s.n.* (PE), *Yamatsuta 84* (TNS), *85* (TNS), *94* (TNS), *104* (TNS), *114* (TNS), *290* (TI); Donglin, *H. Gu et al. 249* (MO), *257* (MO), *263* (MO), *264* (MO), *265* (MO), *267* (MO), *269* (MO), *T. N. Liu et al. 338* (IFP), *C. S. Wang et al. 3772* (IFP, PE, WUK), *Y. L. Zhang 2292*

(IFP), *Kitagawa s.n.* (TI); Xiuyan Xian, Tangchi-xiang, Toudao-dadui, Xiaozhezigou, *W. Wang et al. 454a* (IFP); Zhangwu Xian, Namuqiantu-cun, *T. Wang et al. 2721* (IFP). **Nei Mongol:** Hulun Buir Meng, Ergun Youqi, Shangkuli, *Kitagawa s.n.* (TI); Ju Ud Meng, Hexigten Qi, Guangxingyuan-gongshe, 1200 m, *Mengning Team 1150* (PE). **Hebei:** Badaling, *Sato 8870* (IFP, KYO, PE); Beidaihe, *Cowdry 119* (K), *Schnack 135d* (W); Changli Xian, *W. Y. Hsia 1945* (E); Changshanyu, *Nakai et al. s.n.* (TI); Dongling-shan, Hongsongken, *H. F. Chow 40593* (PE); Jizhou Xian, "Pan-shan," *Y. Yabe s.n.* (PE); "Paita," 1015 m, *Licent 9* (W); Shanhaiguan, Jiao-shan, *1579* (BM, P, W); Xinglong Xian, Wuling-shan, Hongmeisi, 650 m, *P. Y. Fu et al. 4568* (IFP, PE), *Nakai et al. s.n.* (TI); from Chaihekou to Xinglongtang, *Nakai et al. s.n.* (TI); from Xinglongtang to Beiyingfang, *Nakai et al. s.n.* (TNS), *Clemens 4153* (E). **Beijing:** Changping Xian, Xiakou, Xigou, *PE Team 1585* (PE); Gubeikou, Wuohu-shan, *Sato 10287* (IFP, PE); Qinglongqiao, *Kanasiro 4130* (KYO).

4. **Kalimeris indica** (L.) Sch.-Bip., in Zoll., Syst. Verz. 125. 1854 ["*Calimeris*"]. *Aster indicus* L., Sp. pl. 876. 1753. *Asteromoea indica* (L.) Blume, Bijdr. 901. 1826. *Boltonia indica* (L.) Benth., Fl. Hongk. 174. 1861. TYPE: China: without locality (holotype, *LINN-997/42* not seen; photos, GH, NY; microfiche, MO).

Matricaria cantoniensis Lour., Fl. cochinch. ed. 1: 498. 1790. *Hisutua cantoniensis* (Lour.) DC., Prodr. 6: 44. 1838. *Asteromoea cantoniensis* (Lour.) Matsum., Nippon shokubut-sumei ed. 2: 41. 1895. TYPE: China. Guangdong: Guangzhou; type not located.

Martinia polymorpha Vaniot, Bull. Acad. Int. Géogr. Bot. 12: 32. 1903. *Kalimeris indica* f. *polymorpha* (Vaniot) Kitam., J. Jap. Bot. 19: 340. 1943. *Kalimeris indica* var. *polymorpha* (Vaniot) Kitam. ex Y. Ling, in Y. Ling et al., Fl. reipubl. popularis sin. 74: 102. 1985. TYPE: China. Guizhou: Guiyang, 31 July 1897, *E. Bodinier 1739* (lectotype, designated by Lauener (1976), E; isolectotypes, E, P (two sheets)).

Hisutua serrata Hook. & Arn., Bot. Beechey Voy. 265. 1838. TYPE: Japan. Ryukyu Islands: type not located.

Kalimeris indica f. *epapposa* J. Q. Fu, Bull. Bot. Res., Harbin 3: 111. 1983. TYPE: China. Shaanxi: Kang Xian, Qing-he Forestry Station, 1340 m, 18 Oct. 1963, *Z. Y. Zhang 17324* (holotype, WUK).

Root fibrous; rhizomes stoloniferous, 0.5–18 cm long. Stem green or purplish, (12–)20–150 cm tall. Cauline leaves linearly oblong, oblong, oblanceolate, or obovate, entire to deeply pinnate- or lanceolate-lobed, (0.7–)2–7(–9) × (0.3–)0.5–1.8(–2.5) cm, glabrous, or densely covered with ascending thin or thick nonglandular hairs, sometimes with scattered biseriate glandular hairs. Capitula 8–120; peduncles (0.3–)1–9(–13) cm long; bracts 1–8(–12) along the peduncle, the lower ones 6.2–19(–27) × 1–4(–6) mm, the upper ones 1.2–6.3 × 0.2–0.9(–1.3) mm; involucre hemispherical, rarely campanulate, 4.5–10 mm broad, 3–6 mm high. Phyllaries in 3–4 whorls, imbricate, usually obtuse at apex, sometimes purplish; those of outermost whorl lanceolate or obovate, 1.6–3.7(–4) × (0.5–)0.8–1.1(–1.4) mm, those of middle whorl(s) oblanceolate, obovate, or spathulate, 2.3–5.4 × 0.7–2 mm, those of inner whorl oblong to obovate or spathulate, 2.5–5.7 × 0.8–2 mm. Receptacles convex, 1.1–1.7(–2.5) × 0.5–0.9(–1.2) mm. Ray florets 10–26; corollas pale lilac to pale purple; ligules narrowly oblong or oblanceolate to elliptical, glabrous or rarely with scattered long biseriate glandular hairs near the corolla tube, 5.2–16 × 1–3.2 mm, the tube 0.4–2 mm long; style 1.3–2.6 mm long, the branches 0.4–1.3 mm long. Disc florets 40–105; corollas 2.2–4.2 mm long, the lobes subequal or unequal, the longer one (0.8–)1–1.4(–1.7) mm long, the shorter ones 0.6–1.2(–1.4) mm long, both 0.4–0.6 mm wide; the tube 0.6–1.2(–1.5) mm long; anther 0.8–1.6 mm long; style 1.7–3.8 mm long, the branches (0.4–)0.5–1.1(–1.4) mm long, each with a triangular appendage 0.2–0.4 mm long. Ray and disc pappus bristles equal or unequal; ray bristles (0–)0.1–0.3 mm long; disc bristles (0–)0.1–0.3(–0.5) mm long. Achenes brownish to dark purple, obovate to broadly obovate, covered with 4-celled nonglandular hairs and with biseriate glandular hairs at the top, the margins 0.1–0.3 mm broad; ray achenes 3(–4)-ribbed, 1.5–2.6 × 0.6–1 mm; disc achenes 2(–3)-ribbed, 1.5–2.9 × 0.7–1.4 mm. Chromosome number: $n = 18, 27$. Figure 14.

Phenology. Flowering period: May to November.

This is a very variable and widely distributed species. It ranges from central China to South Korea and Japan, and to northern Indochina. It is here divided into three subspecies, as follows:

KEY TO THE SUBSPECIES OF *KALIMERIS INDICA*

1a. Leaves glabrous or loosely covered with thick nonglandular hairs ..... 4a. subsp. *indica*

1b. Leaves densely to evenly covered with thin or thick nonglandular hairs and with scattered glandular hairs.

2a. Cauline leaves obovate to oblong, covered with thick nonglandular hairs; phyllaries of middle whorl(s) ⅓–⅔ as wide as long; rhizomes 5–15 cm long ..... 4b. subsp. *collina*

2b. Cauline leaves lanceolate to oblong, covered with thin nonglandular hairs; phyllaries of middle whorl(s) ⅕–⅓ as wide as long; rhizomes 0.5–1(–3.5) cm long ..... 4c. subsp. *stenolepis*

Figure 14. *Kalimeris indica.* A–E. *K. indica* subsp. *indica.* —A. Upper branch. —B. Root. —C. Achene. —D. Leaf. —E. Portion of leaf showing indumentum. F, G. *K. indica* subsp. *collina.* —F. Achene. —G. Leaf. —H. Portion of leaf showing indumentum. I–K. *K. indica* subsp. *stenolepis.* —I. Achene. —J. Leaf. —K. Portion of leaf showing indumentum.

4a. **Kalimeris indica** subsp. **indica**

Boltonia indica var. ["β"] *rivularis* Hance, Ann. Sci. Nat., Bot. sér. 5, 5: 219. 1866. TYPE: China. Fujian: Fuzhou, 1857, *W. Gregory s.n.* [sub Hance Herbarium Number *1236*] (lectotype, here designated, BM).

Kalimeris indica var. *stenophylla* Kitam., J. Jap. Bot. 19: 340. 1943. TYPE: China. Jiangsu: Nanjing, Zijinshan, 3 Sep. 1934, *H. Migo 40* (lectotype, here designated, TI).

Kalimeris lancifolia J. Q. Fu, Bull. Bot. Res., Harbin 3: 112. 1983. TYPE: China. Shaanxi: Lueyang Xian, 700 m, *Z. Y. Zhang 17891* (holotype, WUK).

Rhizomes stoloniferous, 0.5–18 cm long. Stem 13–75 cm tall. Cauline leaves oblong, oblanceolate, elliptical, or obovate, serrate to deeply pinnate-lobed or less often entire, (1.7–)2.4–7.5(–9) × (0.3–)0.7–1.8(–2.5) cm, glabrous or with scattered thick nonglandular hairs and biseriate glandular hairs abaxially, less often adaxially, lobes lanceolate, 0.9–2.1 × 0.2–0.4 cm. Capitula 8–30; peduncles 1–10 cm long; bracts 2–7(–9) along the peduncle, the lower ones 10.2–27 × 1–6 mm, the upper ones 1.6–6.3 × 0.3–1.1 mm; involucre hemispherical or campanulate, 4.5–10 mm broad, 3–6 mm high. Phyllaries imbricate, green, sometimes purplish; those of the outermost whorl 1.6–3.4(–4) × 0.6–1.4 mm, those of the middle whorl(s) (2.3–)2.8–4.5(–5.5) × 1–1.9 mm, those of the inner whorl 3–5(–5.5) × 0.9–1.8(–2) mm. Receptacles 1.3–1.7 mm wide, 0.6–0.9 mm high. Ray florets 10–58; corollas lilac to pale purple, ligules 8–16 × 1.5–2.8 mm, the tube 1–2 mm long; style 1.7–2.8 mm long, the branches 0.5–1.1 mm long. Disc florets 40–105; corollas 2.6–4.2 mm long, the lobes unequal, the longer one 1–1.7 mm long, the shorter ones 0.6–1.2 mm long, both 0.4–0.6 mm wide, the tube 0.6–1.2(–1.5) mm long; anther 0.9–1.6 mm long; style 2.4–3.8 mm long, the branches 0.5–1.1 mm long. Ray and disc pappus bristles similar, (0–)0.1–0.3 mm long. Achenes purplish, the margins 0.1–0.3 mm broad; ray achenes 2.1–2.6 × 0.6–1 mm; disc achenes 2.1–2.9 × 0.9–1.4 mm. Chromosome number: $n = 27$. Figure 14A–E.

Phenology. Flowering period: June to early November.

Distribution (Fig. 15). *Kalimeris indica* subsp. *indica* is one of the most widely distributed taxa in *Kalimeris*, overlapping the ranges of the other two subspecies of *K. indica* almost completely (it does not occur on Hainan Island). In China, it extends from Qingdao, Shandong, westward to the Qinling Mountains, southwestward to the foot of the Qingzang Plateau, and occurs in all provinces of East and South China (Shanxi, Henan, Shaanxi, Ningxia, Gansu, Anhui, Jiangsu, Zhejiang, Jiangxi, Fujian, Taiwan, Guangdong, Guangxi, Hunan, Hubei, Sichuan, Guizhou, and Yunnan). It also occurs in southern Korea, in Junnam province and extending to Cheju Island. In Japan, it occurs on Kyushu (Nagasaki and southern Kagoshima prefectures), and on the Ryukyu and Ogasawara Islands. In Southeast Asia, it is found in northern Vietnam (Dong Dang, Langson, and Hung Hoa), northern Thailand (Phitsanulok and Chiang Mai), northern Burma (N'changyang), and Malaysia (Melaka). It has been reported in Laos (Gagnepain, 1924), but no authentic material has been seen. Collections from Java are cultivated material (Miquel [1856] reported this taxon in cultivation in Sumatra and Java), and a recent collection from Oahu, Hawaii (*Wagata 2457*, K), may be a plant escaped from cultivation. This subspecies occurs over a very broad altitudinal range as well, from near sea level to 3900 m in Yunnan, although it primarily occurs below 2000 m. *Kalimeris indica* subsp. *indica* is strongly associated with human activities. It grows primarily along sunny, dry roadsides, margins of crop fields, and semi-cultivated places near houses. It can also be found in more stable natural environments, such as margins of thickets or openings in forests, where its populations are often large due to the extensive formation of rhizomes.

Figure 15. Geographical distribution of *Kalimeris indica* subsp. *indica*.

Boltonia indica var. *rivularis* Hance was published without a designated type specimen. There are several specimens with the same Hance Her-

barium number, *1236*, collected at different localities. The only one annotated by Hance with that name is the specimen chosen here as the lectotype. The other Hance collections with this number are from Guangdong Province, China (Nov. 1860, BM; Dec. 1860, GH; 1860, W, two sheets).

Like that of other taxa in this genus, the leaf morphology of this subspecies is very variable, ranging from entire to deeply pinnate-lobed. Populations found on islands, peninsulas, or along the sea coasts tend to comprise short plants with broad, crenate leaves, whereas plants from the continental interior have various kinds of leaves. Individuals with deeply pinnate-lobed leaves have been found scattered throughout the geographic range. Several specimens have been misidentified as *K. pinnatifida* or *K. mongolica*, mainly because of their deeply pinnate-lobed leaves (e.g., *I. B. Balfour s.n. in 1910*, E). Such plants have been accorded taxonomic recognition as *K. indica* var. *polymorpha* (Vaniot) Kitam. ex Y. Ling, but no other character states are consistently associated with this leaf character. Some plants from Yunnan, the western limit of this subspecies, have narrowly oblong and entire leaves and are less branched (*Forrest 28457*, BM, M, and *30584*, BM; *Y. Tsiang & H. Wang 16414*, A; *H. C. Wang 4093*, PE); again, there are no other character states consistently associated with these characters. *Kalimeris lancifolia* J. Q. Fu was based on one specimen from Lueyang, Shaanxi, which is very similar to the narrow-leaved individuals from Yunnan. All these collections have been assigned to *K. indica* subsp. *indica* in the present treatment. Kitamura published a variety, *Kalimeris indica* var. *stenophylla*, based on the individuals with narrower leaves. Some of the specimens cited by him clearly belong to *K. indica* subsp. *stenolepis*, and some to *K. indica* subsp. *indica*.

The length of the pappus is another variable character in *K. indica* subsp. *indica*, as is the case in several other species of *Kalimeris*. Some populations from Yunnan have longer pappi or pappi with united bases, conditions rarely found in populations from other localities; but these character states are not consistent even within populations. For example, one collection from eastern Yunnan (*Forrest 22424*) has duplicates with both longer (about 0.4 mm, E) and shorter (about 0.2 mm, P) pappi. These populations are distributed at the margin of the range of the taxon, where extreme variations are to be expected. Epappose individuals also occur sporadically throughout the entire geographic range.

This taxon is sympatric with *Kalimeris integrifolia* in Hubei and Jiangsu, the southern limit of the latter taxon. It is also often sympatric with *K. shimadai*. No intermediates have been observed in the areas where their populations occur virtually mixed together.

Kalimeris indica subsp. *indica* is sympatric with subspecies *stenolepis* in central China, and with subspecies *collina* in southern China, usually in open areas or at lower elevations in montane regions. In Wuchang, Hubei, and Lueyang, Shaanxi, the senior author found nearly co-occurring populations of subspecies *indica* (mostly in more sunny, disturbed, and drier places) and subspecies *stenolepis* (in relatively mesic and protected areas). Based on herbarium information, subspecies *indica* and *collina* are sympatric in South China. The latter tends to grow in more mesic areas when it is co-occurring with the former. These three subspecies are distinguished mainly by indumentum, branching pattern, and morphology of involucre and pappi (Fig. 14).

The young rosettes of this subspecies are edible as a salad (GH, pers. obs.) and leaves are used in some areas as a folk medicine (Anonymous, 1990). Because it is often cultivated for these purposes, the wide range of this plant may be due in part to cultivation and occasional naturalizing.

Additional specimens examined. CHINA. **Shanxi:** Hengqu Xian, Tongshan-gongshe, Sanliyao, *K. T. Fu 18643* (WUK), Yangshulin, 900 m, *Smith 6180* (W), Yecho-shan, 1500 m, *6429* (BM, W); Jincheng Xian, *S. Y. Bao & S. J. Yan 2209* (WUK); Qinshui Xian, Xiachuan-gongshe, Zhuwugou, 1700 m, *K. T. Fu 18301* (WUK); Xiachuan, Yaoshan, 1500 m, *Licent 12526* (W). **Shaanxi:** Baocheng Xian, Hedongdian, *K. T. Fu 5513* (PE, WUK); Baoji Xian, Hudian Railway Station, 820 m, *13859* (WUK); Hu Xian, Zhifanggou, *B. Z. Guo 48* (PE); Huaying Xian, Wongyu, 420 m, *Huangtugaoyuan Team 1276* (WUK); Huangling Xian, Diantou-gongshe, Laohuzui, 1050 m, *487* (WUK); Huanglong-shan, Fengjiahe, *K. T. Fu 3436* (WUK); Langao Xian, Silihe, from Diushan to Chapeng, 1800 m, *P. Y. Li 8439* (KUN); Lantian Xian, Balongmiao, 1200 m, *T. P. Wang 15931* (PE, WUK); Lueyang Xian, Baiquesi, *C. L. Tang 561* (WUK), Guojiaba, *K. T. Fu 5912* (PE, WUK), from Jiangzheng to Maliutang, 760 m, *C. L. Tang 399* (HIB, KUN, PE, WUK), from Wangjiatuo to Lueyang, Jialing-jiang River, *H. Gu & Q. Han 205* (MO), *219* (MO); from Lueyang to Wujiaying, 520 m, *K. T. Fu 5965* (PE, WUK); Mei Xian, Taonggujiaokou, *R. M. Zhang 679* (KUN, WUK); Mian Xian, Dingjun-shan, 900 m, *P. Y. Li 378* (WUK); Ningqiang Xian, Liejinba, 780 m, *42* (KUN, WUK), Simodi-gongshe, 950 m, *J. Q. Xing 9660* (WUK), 760 m, *T. N. Liu & C. Wang 107* (PE, WUK); Pingli Xian, Pingli-zheng, 1150 m, *P. Y. Li 1710* (WUK); Shangnan Xian, Jiangxigou, 1000 m, *S. B. He 547* (WUK), 400 m, *735* (WUK); Mt. Taibai-shan, Baiyunshagou, *Z. P. Wei 1047* (WUK), Baiyunxiamen, 1030 m, *K. T. Fu 8758* (WUK), Taochuan, Lingdanmiao, Zaoyuan, 1400 m, *9764* (WUK); Yang Xian, Huayang, *B. Z. Guo 1839* (PE, WUK); Niulingbaigou, *T. N. Liu & P. C. Tsoong 3668* (PE), Yuanjia-zhuang, 1300 m, *J. X. Yang 2085* (WUK); Zhongnan-

shan, 1500 m, *H. W. Kung 2845* (PE), *Y. Y. Pai 1168* (PE); Ziyang Xian, from Songshu Xian to Banjiuguan, *P. Y. Li 4843* (WUK). **Gansu:** Hui Xian, Danjiazhang, 600 m, *Z. P. Wei 2044* (WUK), Taishanmiao, 900 m, *1966* (WUK); Pingliang Xian, Kongtong-shan, *Huanghe and Ganyi Teams 1835* (PE), *1939* (PE); Wen Xian, Bikougongshe, 750 m, *Z. Y. Zhang 13029* (WUK), 950 m, *13732* (WUK), Caohebaxiagou, 1300 m, *9240* (WUK), 1500 m, *11802* (WUK), Danbao-gongshe, Gudaopingshan, 950 m, *8827* (WUK), from Hua-zai to Tiewui-zai, 1100 m, *10815* (WUK); Shifang-gongshe, 1100 m, *7065* (WUK), Songping-dui, 1200 m, *6573* (WUK), Zhongzaigongshe, Dahai-dui, Dongshan, 1000 m, *6366* (WUK), 2500 m, *6839* (WUK), 1800 m, *7094* (WUK), 3000 m, *7884* (WUK); Wudu Xian, from Cike to Fenghuang-shan, 1660 m, *3541* (WUK), 1800 m, *3789* (WUK). **Anhui:** Chaocheng Xian, Dong'an, *Huadong Field Station Team 3773* (PE); Shucheng Xian, Xiaotian, *4274* (PE). **Henan:** Lushi Xian, Wulichuan to Hanhe, Dahegou, alt. 880 m, *J. Q. Fu 565* (HIB, WUK); Ye Xian, *R. C. Ching 8679* (E, PE). **Zhejiang:** Tianmu-shan, *T. Hong & P. K. Keng 348* (KUN), *Y. W. Law 1220* (PE), Chanwasi, 400 m, *Zhejiang Expedition Team 28893* (PE), *29121* (PE), *29159* (PE); Taishun Xian, Wenping, *S. Y. Zhang 3617* (PE). **Jiangxi:** Duchang Xian, Shangshou-cun, *F. Maekawa 119228* (TI); Gan Xian, Huangpodi, 630 m, *Z. B. Yang & J. Yao 1164* (PE); Jiujiang Xian, *Allison 4* (GH), *Sherrer s.n.* (K); Xiushui Xian, Moshagang, Qingliang-shan, 300 m, *S. S. Lai 3134* (PE). **Fujian:** Gu-shan, *H. H. Chung 7596* (A). **Hubei:** Badong Xian, *Henry 2474* (K), 300 m, *R. H. Huang 56* (HIB, WUK), *1070* (HIB, WUK), 200 m, *T. P. Wang 10791* (PE, WUK); Echeng Xian, *H. C. Chow 378* (NY); Fang Xian, Dongxidian, Baiguoshupo, 1000 m, *J. Q. Xing 17990* (HIB, WUK), Dayaping, 1000 m, *17789* (HIB, WUK), Guanjingdong, 850 m, *K. M. Liu 8995* (PE), *9039* (PE), *9048* (PE), Yangriwan, 340 m, *K. R. Liu 393* (HIB, PE); Fengjie Xian, Shuangdian-xiang, Guanmenshan, 590 m, *M. Y. Fang 24785* (HIB), 800 m, *24915* (HIB), Fuchikou, *H. C. Chow 207* (NY); Hankou Shi, *Michaelis 78* (W); Hefengcheng, Daping-nongchang, *H. J. Li 6246* (HIB, PE), Jigongdong, 310 m, *H. J. Li 6493* (HIB, PE), Erqu-qincaoping, 440 m, *6530* (HIB, PE), *6623* (HIB, PE); Jiayu Xian, Huancheng-gongshe, *Q. S. Wang 302* (HIB), *306* (HIB); Jun Xian, Wudang-shan, 1080 m, *J. Q. Xing 10652* (WUK), 1500 m, *12096* (WUK); Caodian, Dashidong, 1400 m, *12738* (WUK, SZ), Huangjintang, 1550 m, *11679* (SZ, WUK), 1610 m, *12619* (SZ, WUK), Jingding, 1500–1700 m, *12820* (SZ, WUK), *13056* (SZ, WUK); Qixingshu, 980 m, *10725* (SZ, WUK), Wuyaling, 1020 m, *10901* (SZ, WUK), Zhufengxigou, 1300 m, *13089* (SZ, WUK), Zixiaodian, 850 m, *10555* (SZ, WUK), 920 m, *10975* (SZ, WUK), 750 m, *11073* (SZ, WUK), 1020 m, *11273* (SZ, WUK); Laifeng Xian, Jiusi, Huangtuxiang, 500 m, *H. J. Li 5307* (HIB, KUN, PE), *5757* (KUN, PE), *7229* (KUN, PE); Lichuan Xian, Maoba, 1000 m, *L. Y. Dai & Z. H. Qian 922* (PE); Moba, *G. X. Fu & Z. S. Zhang 1584* (HIB, PE); Ningshan Xian, Shagou, 1120 m, *Z. W. Zhang 1237* (WUK); Puqi Xian, Shengshan-gongshe, *Q. S. Wang 370* (HIB); Shijian Xian, Jinyanhe, Zuandongyan, 290 m, *L. Y. Dai & Z. H. Qian 425* (PE); Sui Xian, Junchuan, Yao-shan, *X. B. Chen 173* (HIB); Tongshan Xian, Jiugong-shan, Jiugong Forestry Station, *L. Y. Dai et al. 2366* (IBSC); Wuhan Shi, Heyang, Shajiaping, 1180–1200 m, *H. J. Li 8739* (PE), Hongshan, 200 m, *C. C. Chow 55* (A, G, NY), *S. W. Teng 233* (W); Wuchang Shi, Luojiashan, *H. H. Chung 9129* (A, G, NY), *S. C. Sun 830* (NY), Wuhan University, *Fukuoka c-245* (KYO), *c-258* (KYO, TI), Mo-shan, *Fukuoka c-206* (TI), *H. Gu & D. Chen 122* (MO), *X. Z. Long 241* (KYO, TI), She-shan, *Migo 64* (KYO), *Y. Z. Long 254* (KYO); Xianfeng Xian, Disi-qu, Ganhegou, 1000 m, *H. J. Li 9387* (HIB, WUK); Xingshan Xian, *G. X. Fu & Z. G. Zhang 259* (HIB, PE), *260* (HIB, PE), Fenglong-gongshe, Hongxingfengjiagou, 900 m, *Shengnongjia Team 21777* (HIB), Nanyanghe, 700 m, *K. R. Liu 774* (HIB, PE), *1980 Sino-Amer. Bot. Expedition 1105* (A, E, NY); Xuan'en Xian, Piandaoxi, 1000–1100 m, *H. J. Li 4767* (HIB, WUK), *4791* (HIB, WUK); Yuan'an Xian, Hehua-gongshe, *J. W. Wang & F. T. Wu 120* (HIB); Yichang Xian, Longwangdong, 600 m, *T. P. Wang 11322* (HIB, PE, WUK), Sanyoudong, 200 m, *Z. Zheng 101* (HIB, PE), *J. H. Zheng 96* (HIB, PE), *Henry 835* (LE), *1343* (LE), *2099* (G, GH, TI), *2739a* (K); Zhuxi Xian, Dahui, 800 m, *K. M. Liu 8574* (PE), Shuangzhuyuan, 850 m, *K. M. Liu 8692* (PE), *Henry 70* (GH), *1051* (E), 1100 m, *H. J. Li 5486* (HIB, WUK), *Wilson 1693* (K, NY, P, W). **Sichuan:** Fengji Xian, Jiannong-xiang, Hongyandong, 700 m, *Z. R. Zhang 25884* (HIB, KUN, PE), Dukouba, *R. Z. Zhang 25652* (PE), Shuangdian-xiang, *M. Y. Fang 24783* (KUN, PE), *24785* (KUN, PE), Zhuyuan, Gaoshi, 850 m, *H. F. Chou 26593* (KUN, PE), *26886* (KUN, PE), *S. X. Fu 110814* (HIB); Guangyuan Xian, *P. Y. Li 988* (WUK); Jiange Xian, Lianhua-shan, 550 m, *T. N. Liu & C. Wang 342* (WUK); Wushan Xian, *H. H. Chung 1702* (PE), *Henry 7204* (A, GH, K). **Guizhou:** Dejiang Xian, Yanmenkou, 1220 m, *Z. F. Liu & T. P. Zhou 1781* (KUN).

4b. Kalimeris indica subsp. **collina** (Hance) H. Y. Gu, stat. et comb. nov. *Boltonia indica* var. "α" *collina* Hance, Ann. Sci. Nat., Bot. sér. 5, 5: 219. 1866. *Kalimeris indica* var. "α" *collina* (Hance) Kitam., J. Jap. Bot. 19: 40. 1943. TYPE: China. Guangdong: Guangzhou, Oct. 1859, *Hance 5195* (lectotype, here designated, BM).

Rhizomes stoloniferous, 5–15 cm long. Stem green or less often purple, 10–100 cm tall. Cauline leaves obovate to oblong, serrate to lanceolate-lobed, 1.4–5.6 × 0.4–2 cm, densely to loosely covered with thick nonglandular hairs on both sides and with biseriate glandular hairs abaxially. Capitula 15–50; peduncles 1.8–9(–12) cm long; bracts 1–9 along the peduncle, the lower ones 6–9 × 1.1–3.7(–4.5) mm, the upper ones 2.3–5 × 0.2–0.7 mm; involucre hemispherical, 5–9 mm broad, 3–4.5 mm high. Phyllaries imbricate, often densely covered with thick nonglandular and glandular hairs, sometimes purplish; those of the outermost whorl lanceolate or obovate, 1.6–2.9 × 0.6–1.4 mm, those of the middle whorl(s) obovate or spathulate, 2.5–4.5 × 1–1.8 mm, those of the inner whorl obovate to broadly oblanceolate or spathulate, 2.4–4.5 × 0.9–1.5 mm. Receptacles 1.1–1.7 mm wide, 0.5–0.8 mm high. Ray florets 16–25; corollas whitish to lilac, ligules 5.2–10(–13) × 1–2.6 mm, the tube (0.4–)0.8–1.4(–1.8) mm long; style 1.5–2 mm long, the branches 0.6–1.2 mm long. Disc florets (40–)70–102; corollas 2.2–3.8 mm long, the lobes subequal, the longer one 1–1.5 mm long, the shorter ones 0.8–

Figure 16. Geographical distribution of *Kalimeris indica* subsp. *stenolepis* (stars) and *K. indica* subsp. *collina* (dots).

1.4 mm long, both 0.4–0.6 mm wide, the tube 0.6–1 mm long; anther 0.8–1.4 mm long; style 2.2–3.3 mm long, the branches (0.4–)0.7–1 mm long. Ray and disc pappus bristles similar, 0.1–0.3 mm long, or sometimes epappose. Achenes purplish, the margins about 0.1 mm broad; ray achenes 3-ribbed, 1.5–2 × 0.7–0.9 mm; disc achenes 2-ribbed, 1.5–2 × 0.7–1 mm. Chromosome number: $n = 18$. Figure 14F, G.

Phenology. Flowering period: late May to November.

Distribution (Fig. 16). *Kalimeris indica* subsp. *collina* is centered in South China, mainly in Guangdong and Guangxi, just reaching northern Vietnam. It barely overlaps at its northern limit the range of *K. indica* subsp. *stenolepis*. It occurs in the following provinces: Jiangxi, Fujian, Guangdong, Hainan, Guangxi, Hunan, Guizhou, and Yunnan. Its altitudinal range is 200–1700 m, but occurs primarily at lower elevations. It commonly occurs in disturbed habitats, usually along roadsides or at edges of crop fields.

Although Hance did not indicate any specimen when he published *Boltonia indica* var. *collina*, nor in a subsequent article (Hance, 1873) discussing it, the specimen collected by him (Hance Herb. No. *5195*) from Guangzhou (Canton) with his annotation "*Boltonia indica* α Benth. *collina* Hance" is here chosen as the lectotype. Two other Hance collections from the same locality with the same number were collected on different dates, November 1859 (K, W) and October 1863 (W), and lack his annotation.

This subspecies is characterized by its dense, thick, nonglandular hairs and biseriate glandular hairs on the leaves, especially abaxially, on the upper stems and branches, and by its densely disposed peduncular bracts. Its capitula are smaller than those of the other two subspecies, and its ray florets are whitish rather than lilac to pale purple. This taxon has sometimes been misidentified as *K. shimadai* in the herbarium because of its robustness and relatively dense hairs. But its smaller heads, short and thick hairs, and elongated rhizomes distinguish it from *K. shimadai*.

Additional specimens examined. CHINA. **Jiangxi:** Anfu Xian, Wugong-shan, Wenjia, 320 m, *J. S. Yue et al. 2826* (KUN, PE), Kenzhichang, *S. S. Lai 1797* (PE); Dayu Xian, Guba, 500 m, *M. X. Nie et al. 9650* (KUN); Huichang Xian, Fucheng-xiang, Bankenshe, *Q. M. Hu 3375* (IBSC, KUN, PE); Longnan Xian, Wuchi-shan, Linwu-cun, *S. K. Lau 4757* (A, BM, G); Nankang Xian, from Fushi to Dashannao, 340 m, *M. X. Nie et al. 9757* (KUN); Ningdu Xian, *Q. M. Hu 5522* (PE); Ninggang Xian, Dongshang-gongshe, 300 m, *S. S. Lai et al. 5290* (KUN); Quannan Xian, Dongli-xiang, Xikenzhang, *S. K. Lau 4097* (A, G), from Lishuxia to Shangying, 330 m, *Jiangxi Teachers' College Team 12037* (HIB); Shicheng Xian, Kuangkou-xiang, *Q. M. Hu 44617* (PE); Suichuan Xian, Dafenghou, Linyang, 670 m, *Q. S. Yue et al. 3865* (PE), from Nanjiangkou to Youduqiao, *Q. F. Liu 30164* (PE); Xunwu Xian, Jianxi-gongshe, *J. S. Yue et al. 1706* (PE). **Fujian:** Dehua Xian, Leifeng-xiang, *K. M. Wu 60435* (IBSC); Fuzhou Shi, Lingpu-shan, *T. S. Ging 5233* (MO), *5399* (BM, MO), Wushi-shan, *H. H. Chung 2402* (E, G), *Carles 799* (E), *H. H. Chung 3815* (PE); Hua'an Xian, Jiao'an-gongshe, Futian, *K. M. Wu 60165* (IBSC); Liancheng Xian, *Y. Ling 3281* (PE), Guanxiang-shan, *3248* (PE); Minhou Xian, Gu-shan, *H. H. Chung 2326* (A, MO, W), *C. C. Tang & S. E. Ma 2906* (A), *S. G. Tang 5706* (BM, MO); Nanjing Xian, Dalingnan-shan, *Q. F. Guo 140036* (IBSC), *Xiamen University Team 333* (PE); Sha Xian, *Q. L. Chen 65* (PE), *Fujian Botanical Expedition Team 53428* (IBSC, WUK), *P. C. Tsoong 26* (PE); Shaowu Xian, Guandun, *H. N. Fan 9784* (A), Nanbao, *9728* (A), Nantian, *9718* (A), Tieyang, *9588* (A), Xiaping, *9557* (A), *9610* (A), Xieshuken, 1250 m, *9654* (A), Zhangjia, 1170 m, *9623* (A); Yong'an Xian, Baizhangyan, *Y. Ling 2965* (PE), Maoping, *2174* (PE). **Guangdong:** Conghua Xian, from Lumuhe-shuitang to Xiaoshui, *L. Deng 8419* (KUN); Dapu Xian, Fengxi Forestry Station, 500 m, *X. W. Wang et al. 192* (IBSC, PE), Gucun-xiang, *L. Deng 5081* (IBSC, PE), Shenpuchengzheng, Wenfushe, *X. G. Li 202806* (IBSC, PE), Tonggushan, *W. T. Tsang 21594* (A, GH, IBSC, K, KYO, LE, NY, PE); Guangzhou Shi, *Sampson s.n.* (BM), South China Institute of Botany, *H. H. Ye 462* (IBSC), *Rechinger 2260* (W), *Y. Tsiang 3282* (NY); Hainan Island, Baisha Xian, Yayi-xiang, Yaguanglu, *H. D. Zhang 1929* (IBSC), Dan Xian, Meiyang-cun, *W. T. Tsang 776* (A, G, K, NY,

PE); Huidong Xian, Pingshan-gongshe, Chenshuishangjiao, *B. Y. Chen et al. 221* (IBSC); Jiaoling Xian, Changtan, *X. H. Xu & H. F. Lin 153866* (IBSC), Nanlixiang, Sanxijiang, *X. G. Li 202385* (IBSC); Lechang Xian, Beixiang-qu, *N. C. Dong 1472* (KUN), *S. Q. Chen 1472* (PE), Beixiangqu Forestry Station, *H. Gu & Z. Li 306* (MO), *307* (MO), *308* (MO), *309* (MO), *310* (MO), *314* (MO); Liannan Xian, Shi-shan, Sanjiang-zheng, 150 m, *P. X. Tan 58868* (KUN, PE), Jinken-xiang, Huangdong, 300 m, *59479* (KUN, PE), Yao'an-xiang, Dapotou, 300 m, *59944* (KUN); Lingyun Xian, Yupi-xiang, *X. Q. Liu 28542* (PE); Luoding Xian, "Kolan," *Y. Tsiang 1189* (GH, NY); Longmen, Nankun Forestry Station, *G. C. Zhang et al. 81* (IBSC), Nankun, Shangpingsanden, *Z. F. Wei 121999* (IBSC, KUN, PE); Maoming Xian, Dapoqu, Gexiang-xiang, *L. Deng 2062* (KUN); Mei Xian, Jiaying, Yingnashan, *W. T. Tsang 21400* (GH, KYO, NY, PE); Ruyuan Xian, Er-qu, Tixiashan, *Z. Huang 42350* (IBSC, SYS); Shantou Shi, *Maclagan 124* (BM); Shixing Xian, Luoba-xiang, Dongxing-she, Da'anken, 300 m, *L. Deng 7027* (KUN, PE), from Luoba-xiang to Huangken, 200 m, *7108* (KUN, PE), Zhangdongshui Conservation Area, *Shixing Team 172* (IBSC); Wengyuan Xian, Diyi-qu, Zhanyuan-xiang, Shangmiao-shan, *X. Q. Liu 25137* (KUN, PE), Huangzhuyi, Qingyun-shan, *S. K. Lan 664* (G, GH, NY), *2152* (GH, IBSC); Xinfeng Xian, Huangpoxiang, Lugushe, 650 m, *L. Deng 7972* (KUN, PE); Xinxing Xian, Tianjie-xiang, Sijialiao-kenshe, *Y. G. Liu 2538* (HIB, PE); Xinhui Xian, Gudou Forestry Station, Wusongkou, *Y. Z. Gao et al. 10* (IBSC); Yangshan Xian, Yangshan, *T. M. Tsui 696* (IBSC, MO, NY, PE, W), Siluxiang, Liantang, 1200 m, *P. X. Tan 60363* (IBC, KUN), *60368* (IBSC, KUN), 1300 m, *60369* (IBSC, KUN); Yangzhun Xian, Yunfu, *Z. Huang 37257* (IBSC, PE), Waicheng, *42103* (IBSC, SYS); Zhaoqing, Dinghu-caochang, *G. L. Shi 13241* (IBSC), Qixing-gongshe, Songxiang-chang, *Guangzhou Qisi Team 4956* (IBSC), Qixingyan, *G. L. Shi 12093* (IBSC); *Levine 3446* (E, G, MO); *T. K. Ping 1884* (E, PE). **Guangxi:** Damiaoshan Xian, Antai-qu, Shaosang-xiang, Yuanbao-shan, *S. Q. Chen 16760* (IBSC, KUN, PE), Sanfang-qu, Luodong-xiang, *14484* (IBSC, KUN, PE), Pingshi-xiang, Jiuxianhenggang, 500–700 m, *16312* (IBSC, KUN, PE); Dayaoshan Xian, 1700 m, *C. Wang 40255* (A); Guilin Shi, Qixingyan, Putuo-shan, 200 m, *Guangxi Team 3760* (PE), Pangu-shan, Chaotian-shan, Sanming-cun, *W. T. Tsang 28036* (A), 220 m, *Chow & Wan 79046* (KYO, NY); He Xian, Babuzheng, *S. Q. Zhong A 60881* (KUN), Gouzitun, *Y. K. Li 401235* (IBSC); Huaiji Xian, Dangshan, *W. T. Tsang 22759* (G, GH, W), Linwang, *S. K. Lau 28542* (A), Tongzhongcun, Touyueshan, *W. T. Tsang 23247* (G, GH, W); Lingui Xian, Dayan-xiang, *S. Q. Zhong A 60092* (KUN), Liangfeng Agriculture College, *C. F. Liang 30624* (PE), Liangfeng-qu, Yan-shan, *Y. B. Xu 10051* (KUN); Longtan, Daqing-shan, Kou-cun, 290 m, *S. Q. Chen 11800* (KUN, PE), Paizong-xiang, 360 m, *14007* (IBSC); Nanping, Nanpingdapuo, *L. S. Ou 150* (IBSC); Shanglin Xian, Qianjiang, *Kimura s.n.* (KYO); Tian'e Xian, Liupai-qu, *Z. Huang 43384* (KUN, PE); Xingdu Xian, Jindayong-cun, Buying-shan, *W. T. Tsang 22994* (G, GH, LE); Wuzhou Shi, *S. Q. Zhong A 62622* (KUN); Yangsu Xian, Yangsu Town, *S. Q. Zhong A 60821* (KUN), *H. Fung 21109* (A); Yong Xian, Dazi, 380 m, *Steward & C. C. Cheo 1077* (G, GH, HIB, NY, P, W). **Hunan:** Lanshan Xian, Yun-shan, Shenglisi, *H. T. Chang 4690* (IBSC); Xinhua Xian, Xikuang-shan, 500–800 m, *Handel-Mazzetti 2694* (A, E, W). **Guizhou:** Anlong Xian, Huali-gongshe, 900 m, *Anshun Team 3221* (KUN, PE); Sibadui, 1180 m, *Guizhou Team 3581* (IBSC, PE, WUK), 1700 m, *3947* (IBSC, PE, WUK); Danzai Xian, Xingren, Chenjiagou, 1300 m, *7412* (IBSC, WUK); Lugong-gongshe, Niyu, 700 m, *8053* (IBSC); Dushan Xian, 400 m, *C. C. Chang 6510* (NY); Guanling Xian, Balinchou, *S. W. Teng 90735* (A); Kaili Xian, Leigongshan, Shizhu-shan, *Qiannan Team 2329* (KUN, PE); Meitan Xian, Yonghe-chang, 900 m, *T. P. Zhou & Z. F. Liu 2421* (KUN, PE); Weng'an Xian, Yonghe-gongshe, Changlin-guan, liqu, *Lipuo Team 2249* (KUN, PE). VIETNAM. **Tonkin:** Langson, *Bois 82* (P), *Eberhardt 3284* (P), *Lecomte & Finet. 93* (P).

4c. Kalimeris indica subsp. **stenolepis** (Hand.-Mazz.) H. Y. Gu, stat. et comb. nov. *Asteromoea indica* var. *stenolepis* Hand.-Mazz., Acta Horti Gothob. 7: 225. 1938. *Kalimeris indica* var. *stenolepis* (Hand.-Mazz.) Kitam., J. Jap. Bot. 19: 340. 1943. TYPE: China. Fujian: Yenping Xian, 4 Aug. 1924, *H. H. Chung 2895* (holotype, W; isotypes, BM, MO, PE).

Kalimeris indica f. *gracilis* J. Q. Fu, Bull. Bot. Res., Harbin 3: 112. 1983. TYPE: China. Gansu: Wen Xian, Bikou-gongshe, Zhu yuanba, 900 m, 9 Sep. 1959, *Z. Y. Zhang 14791* (holotype, WUK).

Rhizomes 0.5–1(–3.5) cm long. Stem green, 45–150 cm tall, densely covered with thin nonglandular hairs and interspersed with biseriate glandular hairs on the upper part, loosely so on the lower part. Cauline leaves lanceolate to oblong, serrate to deeply pinnate-lobed, 3–6 × 0.6–2 cm, densely covered with thin nonglandular and biseriate glandular hairs abaxially, densely or loosely so adaxially, lobes 0.9–2.3 × 0.3–0.5 cm. Capitula 40–100; peduncles 3–9.5 cm long; bracts 4–12 along the peduncle, the lower ones 6.2–19 × 1.1–3.2 mm, the upper ones 1.6–3.6(–5) × 0.3–0.7 mm; involucre hemispherical, 5–7.5(–10) mm broad, 3–6 mm high. Phyllaries imbricate or sometimes loosely so, covered with thin nonglandular and glandular hairs; those of the outermost whorl lanceolate to oblong, 1.9–3(–3.8) × 0.5–0.9(–1.1) mm, those of the middle whorl(s) oblanceolate to obovate, 2.4–5.7 × 0.7–1.4(–1.7) mm, those of the inner whorl oblong, oblanceolate, or obovate, 3–5.7 × 0.8–1.4(–1.8) mm. Receptacles 1.2–2.5 mm wide, 0.5–1.2 mm high. Ray florets (12–)14–25; corollas whitish to pale lilac, ligules narrowly oblong, 6–14 × 1.3–3 mm, the tube 1.1–2 mm long; style 1.5–2.4 mm long, the branches 0.5–1(–1.3) mm long. Disc florets 30–68; corollas 3–4 mm long, the lobes unequal, the longer one 1–1.6 mm long, the shorter ones 0.7–1.3 mm long, both 0.4–0.6 mm wide, the tube 0.6–1.2 mm long; anther 1–1.5 mm long; style 2–3.5 mm long, the branches 0.6–1(–1.4) mm long. Ray and disc pappus bristles subequal to unequal;

the ray bristles 0.1–0.3 mm long; the disc bristles 0.1–0.4(–0.5) mm long. Achenes brownish, the margins 0.1–0.2 mm broad; ray achenes 3(–4)-ribbed, 2–2.5 × 0.7–1 mm; disc achenes 2(–3)-ribbed, 2–2.5 × 0.9–1.3 mm. Chromosome number: $n = 18$. Figure 14I–K.

Phenology. Flowering period: June to late October.

Distribution (Fig. 16). *Kalimeris indica* subsp. *stenolepis* is endemic to China, where it is especially abundant in Hubei and surrounding central China. It occurs in Shanxi, Henan, Shaanxi, Gansu, Anhui, Zhejiang, northern Jiangxi, northern Fujian, Hubei, Sichuan, and Guizhou. Its primary elevational range is 200–2000 m, but it occasionally reaches 3000 m in Sichuan. It usually grows in relatively shady and protected habitats.

The type collection is from Chaping, Fujian, at the southern limit of the range, and as such does not represent the taxon well, since it includes specimens that are shorter and less vigorous than individuals from near the geographic center. Handel-Mazzetti's concept of this taxon was broader than that in the present treatment. He included in it some narrow-leaved plants that we treat as *Kalimeris indica* subsp. *indica*, which has some characters similar to this taxon but differs by its glabrous, thicker leaves and broader phyllaries. Some specimens cited by him (e.g., *Tang and Hsia 196* and *Bois-Reymond 805a*, W) doubtlessly belong to subspecies *indica*.

Some plants from Jiujiang, Jiangxi (e.g., *Allison 4*, GH; *Migo 46*, KYO; *Sherrer s.n. in 1873*, K) have less hairy leaves and relatively elongated rhizomes, which are not typical for this subspecies, but other characters indicate that they should be included in subspecies *stenolepis*. The pappus bristles of this taxon tend to be conspicuous and are often united at the bases. Two collections from Hubei, *H. C. Chow 378* (NY) and *Henry 2099* (GH, TI), have pappi up to 1 mm long.

Additional specimens examined. JAPAN. **Nagasaki:** Nagasaki Shi, *H. Ando 27* (MAK). **Kagoshima:** Ohshima Gun, Amamiohshima, *Ito 510* (TNS); Tarumizu Shi, Shinmidoo, from Kami-shinmidoo to Horikiri, 50–500 m, *Murata 11496* (TI). **Okinawa:** Ishigaki Shi, Ishigakijima, *Iwasaki 2* (KYO), *Yamasaki s.n.* (TI); Itoman Shi, *Furuse 1589* (K); Kikai Island, *Miyagi 7277* (MAK), between Gusuku and Hyakunodai, *Yoshinaga 523* (MAK); Nago Shi, Harano, *Kanasiro 18* (KYO), Yaedake, 400 m, *Yamazaki s.n.* (TI); Naha Shi, Hantagawa, *Amano 6806* (KYO, TI, TNS), Yogi Agricultural Inst., *Walker et al. s.n.* (KYO); Okinawa Shi, Nishihara, *Tawada 3* (KYO); Okiyerabu-shima, *Ohba 48* (KYO); Shimajiri Gun, Itoman-shi, *Koidzumi s.n.* (KYO); Shuri, *Hatusima 17309* (TI); Yoron Island, Chabana, *Tagawa & Iwatsuki 2442* (KYO), *Hatusima & Sako 30887* (MAK). KOREA. **Junnam:** Damyang, *Boku s.n.* (KYO); Namwon, *Mori 335* (TI). Cheju Island: Mallaisan, *Taquet 226* (BM, E, G, W), *Taquet 9679* (TI), *Nakai 6520* (TI). CHINA. **Shanxi:** Hongtong Xian, Tong-pu railway, *T. Kanasiro 4757* (KYO, PE). **Shandong:** Qingdao Shi, Zhongshan Park, *H. Gu & Y. Gao 292* (MO, PE), *293* (MO, PE), *293a* (MO, PE), *295* (MO, PE). **Henan:** Lushi Xian, Laochun-shan, *K. M. Liu 4842* (PE), 380 m, *J. Q. Fu 365* (KUN, WUK); Luanchuan Xian, Shifangyuan, *Henan Team 2080* (PE); Luoyang Xian, *K. S. Hao 37699* (PE). **Shaanxi:** Ankang Xian, Huohe-gongshe, 1100 m, *P. Y. Li 7928* (KUN, WUK), Langao-gongshe, Shangyixiang, *8631* (KUN, WUK); Baocheng Xian, Huangguanling, *Y. L. Qiao 353* (WUK); Feng Xian, Huangniupu, Huji-shan, *Z. Y. Zhang 189* (HIB, KUN, PE, WUK); Foping Xian, Gaojiaba, 1150 m, *K. T. Fu 4945* (PE, WUK); Langao Xian, Hengbin River, 1800 m, *P. Y. Li 8153* (KUN, WUK), Tiefo-gongshe, 1800 m, *8512*, (KUN, WUK); Liuba Xian, Miaotaizi, 1600 m, *K. T. Fu 6326* (PE, WUK), Zibai-shan, 850 m, *6185* (PE, WUK); Ningqiang Xian, Kuanchuan, 800 m, *P. Y. Li 94* (WUK), Liejinba, *14* (KUN, WUK), Yangpingguan, *Y. L. Qiao 108* (WUK), 750 m, *T. N. Liu & C. Wang 50* (PE); Lueyang Xian, from Luotuo-xiang to Lianghekou, 870 m, *C. L. Tang 976* (WUK), from Wangjiatou to Lueyang, 800 m, *H. Gu & Q. Han 206* (MO), *208* (MO); Yanglin-zheng, Weihe River, *H. Gu & X. Hao 6* (MO), *7* (MO), *8* (MO); Pingli Xian, from Pingli to Yaofu-shan, 1200 m, *P. Y. Li 9101* (KUN, WUK), Yaofu-shan, 1200 m, *9178* (KUN, WUK), Weirugongshe, 1800 m, *109010* (KUN, WUK), Zafu-shan, 1500 m, *8723* (KUN, WUK), Zhangbaodian, 800 m, *9635* (KUN, WUK); Qinling Mts., Qinfeng-shan, 1500–1700 m, *Fenzel 136* (W); Shang Xian, 750 m, *T. P. Wang 16022* (PE, WUK); Shiquan Xian, Gangtie-gongshe, Huangguan River, 1020 m, *J. Q. Xing 7992* (WUK); Puhe-gongshe, 840 m, *9342* (WUK), 1010 m, *10308* (WUK), *10063* (WUK); Xixiang Xian, Zha-zheng, 600 m, *P. Y. Li 7574* (WUK); Xianyang Xian, *Fenzel 2471* (WUK); Yang Xian, Huayang, 1350 m, *J. X. Yang 1441* (WUK), *T. N. Liu & P. C. Tsoong 3500* (WUK); Zhashui Xian, Caiyuyao-qu, 1100 m, *X. X. Zhan et al. 1067* (WUK); Zhouzhi Xian, *Pai 1340* (PE); Ziyang Xian, Chengguan-gongshe, Moshigou, *P. Y. Li 7330* (KUN, WUK); Liangmaya, 700 m, *7004* (KUN, WUK); Maoba, 700 m, *7056* (KUN, WUK); Shuanghe-gongshe, 1750 m, *7211* (KUN, WUK), *4791* (KUN, WUK), *4933* (KUN, WUK), *7194* (KUN, WUK). **Ningxia:** Jinyuan Xian, Xisha, *Ningxia Team 1-0228* (WUK). **Gansu:** Hucheng Xian, from Taihe-gongshe to Zu-zhuang, 1400 m, *Z. Y. Zhang 662* (WUK); Guyuan Xian, Wating, 1400 m, *T. P. Wang 17106* (PE, WUK); Kang Xian, Changba, Shijiagou, *Z. Y. Zhang 16908* (WUK); from Dacaochuan to Xiaocaochuan, *W. Y. Hsia 6338* (PE); Tianshui Xian, Baiyanglin, Tangshangoumen, 1600 m, *J. M. Liu 10477* (PE, WUK); Wen Xian, Bikou-gongshe, 900 m, *Z. Y. Zhang 14791* (WUK), 650 m, *Y. Q. He 1102* (PE); Dongjiaheba, *14897* (WUK). **Anhui:** Anqin Xian, *Q. Z. Hu 3* (PE), *Maekawa 741* (TI); Chu Xian, Langyia-shan, *Huadong Field Station Team 3170* (KUN); Guangde Xian, 280 m, *Anhui Expedition Team 3300* (NAS); Huaining Xian, Ganlusi, *Maekawa 9 B34* (TI); Heyuezhou, *7 B54* (TI); Linhu-xiang, *745* (TI); Maohuling, *8 B22* (TI); Huang-shan, *Chow 33* (A, K, KYO, MO, PE, US), from Chuishilin to Tangkou, *T. N. Liu & P. C. Tsoong 2170* (PE), around Tangkou, *2365* (PE); Jiuhua-shan, 520 m, *C. S. Fan & Y. Y. Li 133* (E), 700–800 m, *S. C. Sun 1239* (NY), *1259* (NY); Dongyiesi, *Huadong Field Station Team 4795* (PE). **Jiangsu:** Baoying Xian, Kenzhichang, Nanzha,

S. L. Liu et al. 18 (IBSC); Danyang Xian, *Nanjing Forestry College Team 7800-447* (IBSC); Jinjiang Xian, Zhulinsi, *Migo 37* (KYO); Nanjing Shi, Wutai-shan, *Merrill 1509* (MO); Xiaolingwei, *Matsuda s.n.* (TI); Suzhou Shi, Guanyin-shan, *Migo 44* (KYO); Lushibang, *H. T. Feng s.n.* (GH); Shangfang-shan, *Migo 43* (KYO); Yixing Xian, Longzhi-shan, *W. Z. Fang et al. 102* (IBSC), *C. N. Chen 8603* (W). **Shanghai Shi:** Minhang, *Kimura s.n.* (KYO); Paoshan, *Migo 36* (KYO), Zhelin, *41* (KYO); Shanghai Botanical Garden, *H. Gu & M. Jiang 304* (MO), *Debeaux 120* (P, cultivated), *Faber s.n.* (BM, P, W), *Kimura s.n.* (KYO). **Zhejiang:** Changhua Xian, Longtang-shan, *X. Y. He 26204* (PE), *29842* (PE); Hangzhou Shi, Genshanmen, *Honda 190* (TI, TNS), *638* (TI); Jiuxi, *H. Gu & Q. Li 305* (MO); Lingyin, *Migo 38* (KYO); Longjin, *X. Y. Zhang 1131* (PE), *T. Tang & W. Y. Hsia 196* (PE, W); Zhengzhuling, *S. Y. Zhang 1052* (NAS); Longquan Xian, Jinqi, *6828* (PE), *7107* (PE); Sheng-shan, *4194* (PE); Muganshan, 730 m, *Cheo & Wilson s.n.* (GH); Ningbo Xian, *Faber s.n.* (E); Siming-shan, Sheng-cun, *X. Y. He 24938* (PE), *25882* (PE); Xuedosi, *27448* (PE); Shouchang Xian, Shangcang, *Zhejiang Team 27655* (PE); "Siakan, Fan-chiao," *R. C. Ching 3629* (W); Shujiang Shi, *Migo 35* (KYO); Tonglu Xian, Hengcun-zheng, *S. Chen 1829* (PE). **Jiangxi:** Dexing Xian, Mao-shan, *M. X. Nie 5172* (PE); Guangchang Xian, Tangfan-xiang, Tianyao-she, Taishan, *Q. M. Hu 5297* (IBSC, KUN); Tangwan-gongshe, *J. S. Yue et al. 2181* (KUN); Guixi Xian, Tianhua-shan, 800 m, *S. S. Lai & M. X. Nie 3809* (KUN, PE); Huchang Xian, Hedong, *Q. M. Hu 2966* (PE); Jinggangshan Xian, Jinggang-shan, 730 m, *J. S. Yue et al. 4894* (PE); Jiujiang Shi, Lu-shan, Guling, 1100 m, *Bois-Reymond 805a* (W), *H. C. Cheo 65* (E), *Forbes 43* (BM), *Schindler 308a* (BM, E, K); Hanbokou, 1120 m, *Migo 65* (KYO), *Y. Tsiang 10770* (NY); Lianhuadong, *T. R. Liu s.n.* (KYO); Louxiansi, *K. J. Guan 74457* (PE), *R. C. Ching 10015* (PE), *10260* (PE), *10462* (PE), *S. Xiong 7109* (PE); Xinziyikou, Qianshusi, *M. X. Nie & S. L. Chen 7418* (KUN, PE); Jiujiang Shi, Lu-shan, *Migo 65* (TI), *66* (TI), *Bailey s.n.* (GH), *Carles s.n.* (E), *Forbes 83* (BM), *927* (BM); Lichuan Xian, Wuyi Mts., Deshengguan-nongchang, Maodian-fenchang, *M. X. Nie et al. 3031* (PE); Lianhua Xian, Miaoqian-gongshe, Jinkengdadui, *S. S. Lai 1651* (PE); Libei Xian, Libei Bridge, 300–700 m, *Y. Tsiang 10223* (NY); Lushan Xian, Wuyi-shan, 700 m, *M. X. Nie 4681* (PE); Xikeng, 751 m, *M. X. Nie & S. S. Lai 4152* (KUN, PE); Nanchang Shi, *T. N. Hsiung 539* (GH), *559* (GH), *616* (PE), *X. X. Yang 10836* (PE); Ningdu Xian, Fanxiangping, Xiapinglongkeng, *Q. M. Hu 5522* (IBSC, KUN); Pingxiang Shi, from Xingdian to Matian, 420 m, *Jiangxi Team 835* (PE); Xuande-qu, 120 m, *2419* (PE); Ruijin Xian, Lishupailiantang-she, *Q. M. Hu 4223* (PE); Shangrao Xian, Wufu-shan, 700 m, *M. X. Nie & S. S. Lai 4681* (KUN, WUK); Shuichuan Xian, Dafenqu, Linyang, 670 m, *J. S. Yue et al. 3865* (KUN); Wangxing Xian, Damao-shan, *M. X. Nie & S. S. Lai 5172* (KUN); Zixi Xian, Wuyi Mts., Matoushan-xiang, 500 m, *3508* (KUN, PE, WUK). **Fujian:** Changting Xian, Bei-shan, *Y. Y. Tung 123* (PE); Chong'an Xian, Wuyi-shan, 500 m, *H. C. Chou 4261* (IBSC); Fuzhou Shi, "Chong Chen Sang," *T. S. Ging 6657* (G, MO); northern Fuzhou, *5667* (LE), *7143* (G, MO); Huaipin-xiang, *Migo s.n.* (PE); Qushi-shan, *Nagasawa 66* (TI); Xijin Xian, Shaken, *Fudan University Team 50299* (KUN), *52402* (KUN). **Taiwan:** Danshui Xian, *Faurie 226* (BM, KYO), *1141* (BM, G, GH, KYO), *Nagasawa 523* (KYO, TI), *Oldham 244* (BM, K, NY); Jilong Shi, *Ford 65* (K), *Makino s.n.* (TI); Taibei Shi, "Sekten," *Keng & Kao 1276(1)* (E), Shilin, *Shike s.n.* (TI), *Makino 169* (MAK), *Asai s.n.* (NY), *Makino s.n.* (TNS), *Tanaka 93* (BM, P); Taibei Xian, *Shimada 5471b* (KYO); Yilan Xian, Dali, *5472b* (KYO). **Guangdong:** Congshi Xian, Huogangyuejin-gongshe, 650 m, *L. Deng 8732* (KUN), *8736* (PE); Fengkai Xian, Heishiding Natural Conservation, *B. H. Liang 12882* (IBSC); Fushan Xian, *C. Wenyon 1887* (K); Guangzhou Shi, Zhongshan University, *S. Y. Lau 20551* (IBSC), *Levine 1081* (GH, MO), *Sampson 319b*, (BM); Honam Island, *Levine 272* (A, GH, MO), *Merrill 10021* (GH, NY); Huangpu Xian, Bei-qu, Huangpodong, *C. Huang 165222* (KUN), *Anderson s.n.* (A), *Hance s.n.* (BM, GH, K, P, W; Hance Herb. Numb. *1236*); Lianyang Xian, Lingbei-gongshe, Lutian, *Y. M. Cheng 170542* (IBSC); Lechang Xian, Zhuangyuan-shan, Jinjiufeng, *W. T. Tsang 20844* (K, KYO, MO, NY, PE, W); Aomen (Macao), *Callery s.n.* (G). **Guangxi:** Longlin Xian, Yancha-xiang, 900 m, *C. C. Chang 10678* (KUN). **Hunan:** Wugang Xian, Yun-shan, Nantianmiao, 310 m, *L. H. Liu & G. Z. He 16483* (PE); Xinhua Xian, Xikuang-shan, 500–800 m, *Handel-Mazzetti 2694* (W). **Hubei:** Badong Xian, Xiagugongshe, Baiqiao, 1000 m, *Hubei Expedition Team 24197* (HIB); Shengnongjia, Niudongwan, Dongjiekou, *G. X. Fu & Z. S. Zhang 1145* (PE); Echeng Xian, Taihe-gongshe, *Q. S. Wang 78* (HIB); Ensi Xian, Siqu-xiang, 1000 m, *H. J. Li 4791* (PE), Xinping-gongshe, Hejiadaping, 310 m, *8900* (HIB); Fengjie Xian, Zhuyuan, Gaozhi, 250 m, *H. F. Chou 26953* (HIB); Huangshi Shi, Bao'an, *H. C. Chow 18412* (G, NY); Dayu, *348* (NY); Wuchang Shi, Luojiashan, *S. C. Sun 772* (NY), *849* (NY); Mo-shan, *H. Gu & D. Chen 121* (MO), *127* (MO); Xianfeng Xian, Disi-qu, 1000 m, *H. J. Li 9387* (KUN); Shuishapiag-xiang, 1400 m, *9051* (HIB, PE); Xuan'en Xian, Piandaoxihou-shan, 1000 m, *4767* (HIB, PE); Yichang Xian, Dengcun, 800–900 m, *H. Gu & D. Chen 134* (MO); Xiaoxita, *195* (MO), *200* (MO), *Wilson 1693* (W), *1703* (K, NY, W); Zigui Xian, Kongjiaqiao, 1300 m, *T. P. Wang 11865* (PE, WUK); Wuzhi-shan, *12098* (PE, WUK); Zhuxi Xian, Longdonghe, 830 m, *P. Y. Li 11118* (KUN, WUK); Tangfonggou, 1500 m, *8797* (KUN, WUK), *9427* (KUN, WUK); from Xiaohegou to Shizi-shan, *9976* (KUN, WUK), *Henry 89* (GH), *216* (BM), *384* (GH), *5209* (GH). **Sichuan:** border with Shaanxi Province, *P. Y. Li 785* (WUK); Baoxing Xian, Fumugou, 1100 m, *K. J. Guan & W. T. Wang 2629* (PE); Xikang, *C. Pei 8083* (PE), *T. P. Tsoong 39422* (KUN, PE); Chengdu Shi, Ximen, *W. P. Fang 12360* (A, BM, W), *S. S. Chien 5320* (W), *5948* (E), 500 m, *Legendre 94* (P), *T. P. Wang 8282* (PE); Chengkou Xian, Qigan-shan, Erguai, 1450 m, *T. L. Dai 102239* (PE), *102260* (PE), *102532* (PE), 600 m, *103190* (PE), *106939* (PE), 1300 m, *107099* (PE); Ebian Xian, *S. L. Sun 982* (KUN), *Z. X. Zhao 550* (KUN); Mt. Emei, *C. Y. Chiao & C. S. Fan 208* (A), 2500 m, *S. C. Sun & K. Chang 1170* (A), 2300 m, *1206* (A), 900 m, *1417* (A), 480 m, *1772* (A); Fuhusi, 510 m, *K. J. Guan 1963* (PE), *G. H. Yang 56939* (KUN); Heilongjiang, 900 m, *C. L. Li 1938* (CDIS); Leigongsi, 800 m, *K. J. Guan et al. 725* (PE); Emei Xian, *S. C. Sun & K. Chang 667* (A); Hanyuan Xian, Xianling-shan, 1200 m, *T. P. Wang 887* (PE, WUK), *8910* (PE, WUK); Hechuan Xian, 450 m, *W. P. Fang 1442* (GH); Hongya Xian, Wawu-shan, Shuangdongxi, *Z. W. Yao 4042* (PE); Huili Xian, Huadianzi, 1850 m, *Q. S. Zhao & S. S. Liu 5704* (IBCD); Kangding Xian, Sanyu School, *H. C. Chow 9008* (A); Ximen, *8940* (A); Luding Xian, Tianba-gongshe, 1470 m, *K. J. Guan & W. T. Wang 1594* (PE); Nanchuan Xian, Jinfo-shan, Lancaoba, Longdong, *G. L. Li 63217* (KUN), 1550 m, *63279* (PE); Sanjiaqianfoyan, 550 m, *K. J. Guan et al. 854* (PE); Xiaohenima-cun, *J. H. Xiong & Z. Y. Chou 91840* (PE),

92444 (PE), *94009* (PE); Shizhu Xian, Muping-gongshe, 1100 m, *Y. Chen 2968* (IBCD); Qiyaoshan Forestry Station, 1710 m, *2137* (IBCD); Tianquan Xian, Chengxiang, 1090 m, *D. Y. Peng 45389* (IBCD); Sihang-xiang, Xinzheng-cun, *W. G. Hu & Z. He 12026* (PE); Xinchang-qu, 870 m, *D. Y. Peng 46699* (IBCD); Xingou, *K. J. Guan & W. T. Wang 2264* (PE); Eryin-shan, 1900 m, *X. M. Jiang 35676* (PE); Wanyuan Xian, Zhongting to Fangjiatian, 800 m, *P. Y. Li 6799* (WUK); Tianba-xiang 700 m, *6909* (KUN, WUK); Dazhudong, 820 m, *4223* (WUK), *4420* (WUK), *5501* (WUK), *5560* (WUK), *5620* (WUK), *5963* (WUK), and *6813* (WUK); Wuxi Xian, Gaoyuo-xianggongsuo, 1000 m, *G. H. Yang 65084* (KUN), *P. Y. Li 3308* (WUK); Zhaohua Xian, Shangsi, 900 m, *Z. P. Wei 3855* (WUK); SW Sichuan, SE of Yungning, 3000 m, *Forrest 22424* (E, W). **Guizhou:** Anlong Xian, Longshan-gongshe, Qiaolingying-qu, 1300 m, *Guizhou Team 4107* (IBSC); Anshun Shi, *Anshun Team 1903* (KUN, PE); Biji Xian, Er-qu, Baohexiang, 1300 m, *P. H. Yu 489* (KUN); Ceheng Xian, Huarong, 800 m, *Z. Y. Cao 855* (PE); Rongbei, 1500 m, *Z. Y. Cao 394* (PE); Chishui Xian, *Biji Team 1190* (KUN); Dafang Xian, Baina-qu, Jiulong-shan, 1850 m, *983* (KUN); Dejiang Xian, Heba Forestry Station, 1050 m, *Qianbei Team 2697* (PE); Yanmenkou, *1781* (PE); Fenjinshan, Dahoyan, 900 m, *Steward et al. 450* (E, GH, NY, PE); Guiding Xian, 600 m, *C. C. Chang 5577* (GH, NY, PE, W); Guiyang Shi, *Bodinier 1913* (E, P), *2474* (K); Guizhu Xian, Dangwu, Heishitou, 1150 m, *Chuanqian Team 2076* (PE); Kaili Xian, Xumu-chang, *Qiannan Team 3723* (KUN, PE); Taojiang, Donglei-shan, 800 m, *2329* (KUN); Luhe Xian, Jinjiagai, 1200 m, *Qianbei Team 2336* (PE); Nayong Xian, Juren-qu, 1800 m, *Biji Team 495* (PE); Pingba Xian, Mapei, 1500 m, *Anshun Team 1759* (PE); Pingyuan-qu, Shawqi-xiang, 1000 m, *Z. F. Liu & T. P. Zhu 2697* (KUN); Pu'an Xian, Qingshan-gongshe, Pubei-nongchang, 1800 m, *Anshun Team 1376* (PE); Qingzheng Xian, Puoyan, 1400 m, *Chuanqian Team 1823* (PE); Rongjiang Xian, Jiazuo-xiang, *Qiannan Team 3065* (KUN, PE); Songtao Xian, Ganlong-qu, Hunquan, 750 m, *Z. F. Liu & T. P. Zhou 1439* (KUN, PE); Mu'erxi, 830 m, *1983* (KUN, PE); Xishui Xian, Guandu-qu, Xinhua-zhuchang, 800 m, *Biji Team 1564* (KUN, PE); Xingyi Xian, Tingxiaogongshe, 1300 m, *Guizhou Team 7063* (IBSC), Qingnangongshe, 1500 m, *Anshun Team 665* (PE); Zunyi Xian, Fenghuang-shan, *Chuanqian Team 853* (PE); Liangfengya, 1100 m, *Steward et al. 51* (A, LE, NY). **Yunnan:** Chengjiang Xian, Yangliaoying, 1800 m, *H. Wang 41433* (A, KUN), 1800–2000 m, *Y. Tsiang & H. Wang 16414* (A); Daguan Xian, from Mugan Forestry Station to Mugangongshe, 1700 m, *Diandongbei Team 507* (KUN); Dali Xian, Liujufeng, *H. C. Wang 912* (PE), *4093* (PE); E of Dali, 3300–3900 m, *Forrest 4005* (BM, E), 3000–3300 m, *11539* (BM, W); Dongchuan Xian, 2500 m, *Maire s.n.* (A, G); Eshan Xian, *H. T. Tsai 53509* (A, KUN, PE); Jiangchuan Xian, *B. Y. Qiu 60231* (IBCD); Kunming Shi, Guandu-qu, 1900 m, *77613* (IBCD); Heilongtan, *50787* (IBSC, PE); Huiliuwan, *K. M. Feng 10290* (KUN, PE); Xishan, 1800 m, *B. Y. Qiu 77566* (IBCD); Lufeng Xian, 1700 m, *H. T. Tsai 53573* (A, E, KUN, PE); Lushui Xian, "Maan-tsang, Shenn-mang-yeang," 800 m, *C. W. Wang 80971* (A, KUN, PE); Luanliang Xian, Eryuetianmalin-qu, 1750 m, *Diandongbei Team 772* (KUN), *773* (KUN); Mengzi Xian, "S of Red Sea," 1500 m, *Henry 9754* (E, K, LE, MO, NY); Mingjiulao-zhai, 1800 m, *Y. Y. Hu & S. K. Wen 580599* (KUN); Xichou, 1400 m, *580715* (KUN), *Ledug s.n.* (P); Pingbian Xian, Maoyitou, 1250 m, *T. W. Wang & Y. Liu 82264* (KUN, PE), 1300 m, *T. T. Tsai 60729* (A, KUN, PE), *61066* (A, KUN, PE), 400 m, *62482* (A, KUN, PE), *62827* (A, KUN, PE); Tengchong Xian, Siyuansishi-gongshe, Xiangjiahe, 1750 m, *W. Q. Yi 60-1238* (KUN); Tengyue Xian, *Howell 95* (E, K); Weixi Xian, 2800 m, *T. W. Wang 67644* (A, KUN, PE); Lidiping, 3000 m, *67686* (A, PE, WUK); Yanshan Xian, Tuguo-zhai, 1200 m, *T. W. Wang & Y. Liu 84131* (KUN, WUK); Yanjin Xian, Qinghe River, Pu'er-du, 500 m, *Diandongbei Team 999* (KUN); Guanhe River, *892* (KUN); Yiliang Xian, 1800 m, *B. Y. Qiu 771226* (IBCD); Zhengxiong Xian, San-qu, Guangduoqian-laolin, 1950 m, *P. H. Yu 992* (KUN, PE); *Ducloux 289* (P), *1585* (E), *Forrest 3063* (BM, E), *8312* (E); northern Lijiang valley, 300 m, *13025* (BM, E), *28457* (BM, MO), *30584* (BM), *Maire 50* (BM), *351* (BM), *454* (BM), *525* (BM), *2561* (NY), *2568* (NY), *F. T. Wang 453* (KUN), *2247* (KUN). **Hong Kong:** *Fortune 124* (BM, mixed with *Forbes 43* and *83*), *Hance s.n.* (W). VIETNAM. Dong Dang, *Petelot 400* (P); Hung Hoa, Hanoi, *s.c. 92* (P); Kiendi, Prairie, *Balansa 4498* (P); Langson, *840* (K, P), *Hautefenille 161* (P). THAILAND. Bangkok, Chinese medicine shop, *Kerr s.n.* (BM); northern Chiang Mai, 1200–1685 m, *Iwatsuki et al. T 9428* (KYO); Phitsanulok in Phu Miang Mts., 1400 m, *Shimizu et al. T 11662* (KYO, TNS). BURMA. N'Changyang, 25°50′ N, 97°48′ E, 1600 m, *Kanlback 273* (BM); North Shau States: Lashio, 900 m, *J. H. Lace 5841* (K). MALAYSIA. Malacca, *D. Yuan s.n.* (G). JAVA. Cultivated: *Blume s.n.* (P), *Zollinger 895* (G, P), *899* (G); Beru, *Zollinger s.n.* (G). U.S.A. **Hawaii:** Oahu, Kaneohe, Keaahala Rd., *Nagata 2457* (K).

5. Kalimeris yomena (Kitam.) Kitam., Kiku 40. 1940. *Kalimeris incisa* var. *yomena* Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 13: 311. 1937. TYPE: Japan. Kyoto: Yoshida, *N. Kinashi s.n. in 11/1921* (holotype, KYO; isotypes, TI, TNS).

Root fibrous; rhizomes stoloniferous, 5–38 cm long. Stem green or rarely purplish, 50–180 cm tall. Cauline leaves narrowly oblong, oblanceolate, elliptical, or obovate, serrate, crenate, or deeply pinnate-lobed, 3.5–8.2(–8.6) × 1.1–3(–3.4) cm, glabrous or sometimes with scattered, thick, nonglandular hairs adaxially and evenly or loosely so and with scattered glandular hairs abaxially, lobes 0.6–1.5 × 0.3–0.6 cm. Capitula 10–105; peduncles 1.3–12(–16) cm long; bracts 2–13 along the peduncle, the lower ones narrowly oblong, 7.8–19(–30) × 1–4(–8) mm, the upper ones (0.8–)1.8–5.5(–7) × 0.4–1.5 mm; involucre hemispherical or campanulate, 4.7–10 mm broad, 3.5–7.5 mm high. Phyllaries in 3–4 whorls, imbricate, glabrous or loosely covered with nonglandular hairs, sometimes purplish; those of the outermost whorl lanceolate to obovate, 2.1–4 × 0.7–1.4(–1.7) mm, those of the middle whorl(s) oblong, obovate or spathulate, 2.7–5.5 × 1–2.2 mm; those of the inner whorl oblanceolate, obovate or spathulate, 3.3–5.5 × 1–1.7 mm. Receptacles convex to subconical, 1.1–2.2 (–2.5) mm wide, 0.6–1.3(–1.5) mm high. Ray florets 14–22; corollas pale lilac to pale purple, ligules 6–

18.4 × (1.3–)2.1–4 mm, the tube 1–2 mm long; style 2–3.4 mm long, the branches 0.6–1.2 mm long. Disc florets (33–)51–100; corollas 3.2–4.7 (–5.1) mm long, the lobes unequal, the longer one 1–2.1 mm long, the shorter ones 0.8–1.5 mm long, both 0.4–0.6(–0.7) mm wide, the tube 0.8–1.4 (–1.7) mm long; anther 0.8–1.5 mm long; style 2.7–4.4 mm long, the branches 0.7–1.3 mm long, each with a triangular or rarely broadly lanceolate appendage 0.3–0.5 mm long. Ray and disc pappus bristles whitish or brownish, subequal or unequal; ray bristles (0–)0.2–0.5 mm long; disc bristles 0.2–0.6(–1) mm long. Achenes straw-colored, brownish, or dark purple, obovate or broadly obovate, covered with 4-celled biseriate nonglandular hairs and topped by glandular hairs, the margins 0.1–0.3 mm broad; ray achenes 3(–4)-ribbed, 2.1–3 × 0.8–1.6(–1.9) mm; disc achenes 2-ribbed, 2.2–3.5 × 0.8–2.3 mm. Chromosome number: $2n$ = 40, 41, 43, 45, 61, 62, 63, 66, 68, 69, 70, 71, 72, and 73. Figure 17.

The nomenclature of *Kalimeris yomena* is complicated. *Kalimeris incisa* var. *yomena* Kitam. and *K. yomena* Kitam. were initially described only in Japanese (Kitamura, 1937a), and so were invalidly published (Article 36.1, ICBN, Greuter et al., 1994). In a second article published the same year, *Compositae Japonicae*, Kitamura (1937b) validated the name *K. incisa* var. *yomena* by including a Latin diagnosis. In an obscure book, again only in Japanese, Kitamura (1940) published the combination *K. yomena* (Kitam.) Kitam. for the first time, although it is sometimes attributed to a later publication (Kitamura, 1957), where he published it in Latin.

This species is endemic to Japan and unique cytologically. Pentaploid, heptaploid, and octoploid plants have been detected, and aneupolyploids are also common (Gu, 1989; Gu & Tara, 1990). It comprises three subspecies, as follows:

KEY TO THE SUBSPECIES OF *KALIMERIS YOMENA*

1a. Pappus more than 0.4 mm long; branches flexible ..... 5b. subsp. *angustifolia*
1b. Pappus less than 0.4 mm long; branches stiff.
  2a. Plants no taller than 80 cm, leaves linearly oblong or oblanceolate and covered with thick nonglandular hairs on both sides ..... 5c. subsp. *dentata*
  2b. Plants up to 160 cm tall; if less than 80 cm tall, leaves oblanceolate or obovate, glabrous or loosely hairy on both sides ..... 5a. subsp. *yomena*

5a. Kalimeris yomena subsp. **yomena**

Kalimeris incisa f. *tubulosa* Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 13: 311. 1937. *Aster yomena* f. *tubulosus* (Kitam.) H. Hara, Enum. sperm. jap. 2: 139. 1952. *Kalimeris yomena* f. *tubulosa* (Kitam.) Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 24: 53. 1957. TYPE: Japan. Shimane (Izumo): Kamo, 30 Oct. 1927, *C. Ishikura s.n.* (holotype, KYO).

Kalimeris pinnatifida f. *leucantha* Nakai, Bull. Natl. Sci. Mus. Tokyo 33: 26. 1953. TYPE: Japan. Yamaguchi: Ohkuragadake, 16 Oct. 1949, *T. Nakai & N. Marugama s.n.* (holotype, TNS).

Kalimeris indica var. *grandiflora* Nakai, Bull. Natl. Sci. Mus. Tokyo 33: 27. 1953. TYPE: Japan. Yamaguchi: Yamaguchi Shi, Housenji, 14 Oct. 1949, *T. Nakai & N. Maruyama s.n.* (holotype, TNS).

Rhizomes stoloniferous, 10–38 cm long. Stem 55–120(–160) cm tall; branches usually stiff. Cauline leaves oblong, oblanceolate, elliptical, or obovate, serrate, crenate, or lanceolate-lobed, glabrous, or loosely covered with nonglandular hairs, 3.5–8 × 1.2–3 cm. Capitula 10–90; peduncles 1.3–12(–16) cm long; bracts 2–12 along the peduncle, the lower ones 8–17(–30) × 1–4(–8) mm, the upper ones (0.8–)1.8–5.4 × 0.4–1 mm; involucre 5.5–10 mm broad, 4.2–6.5(–7.5) mm high. Phyllaries in 3–4 whorls, imbricate, sometimes purplish; those of the outermost whorl 2.1–4 × 0.7–1.4(–1.7) mm, those of the middle whorl(s) 2.7–5.5 × 1–2.2 mm, those of the inner whorl 3.3–5.5 × 1–2.2 mm. Receptacles 1.1–2.1(–2.5) mm wide, 0.7–1.2(–1.5) mm high. Ray florets (14–)16–27; corollas lilac or pale purple, ligules 9.4–18.4 × 2.2–4 mm, the tube 1–2 mm long; style 2–3.1 mm long, the branches 0.6–1.2 mm long. Disc florets (33–)51–100; corollas 3.2–4.4(–4.7) mm long, the lobes unequal, the longer one 1.2–2 mm long, the shorter ones 0.9–1.3 mm long, both 0.4–0.6 mm wide, the tube 0.8–1.4(–1.6) mm long; anther 1–1.5 mm long; style 2.8–4 mm long, the branches 0.7–1.3 mm long. Ray and disc pappus bristles subequal, 0.3–0.4(–0.5) mm long. Achenes brownish or dark purple, the margins 0.1–0.3 mm broad; ray achenes 3(–4)-ribbed, 2.1–3 × 0.9–1.6 mm; disc achenes 2-ribbed, 2.3–3 × 1.4–1.9 mm. Chromosome number: $2n$ = 61, 62, 63, 66, 70, 71, 72. Figure 17A–C.

Phenology. Flowering period: June to late October.

Distribution (Fig. 18). Endemic to Japan. This has the widest geographic range of any subspecies of *Kalimeris yomena*. It occurs from Ajigata-mura, Niigata in northern Chubu District, and Saitama and Chiba prefectures in Kanto District south and west to Shikoku and southern Kagoshima of Kyushu. It also occurs on Iki, Fukue, and Yaku Islands,

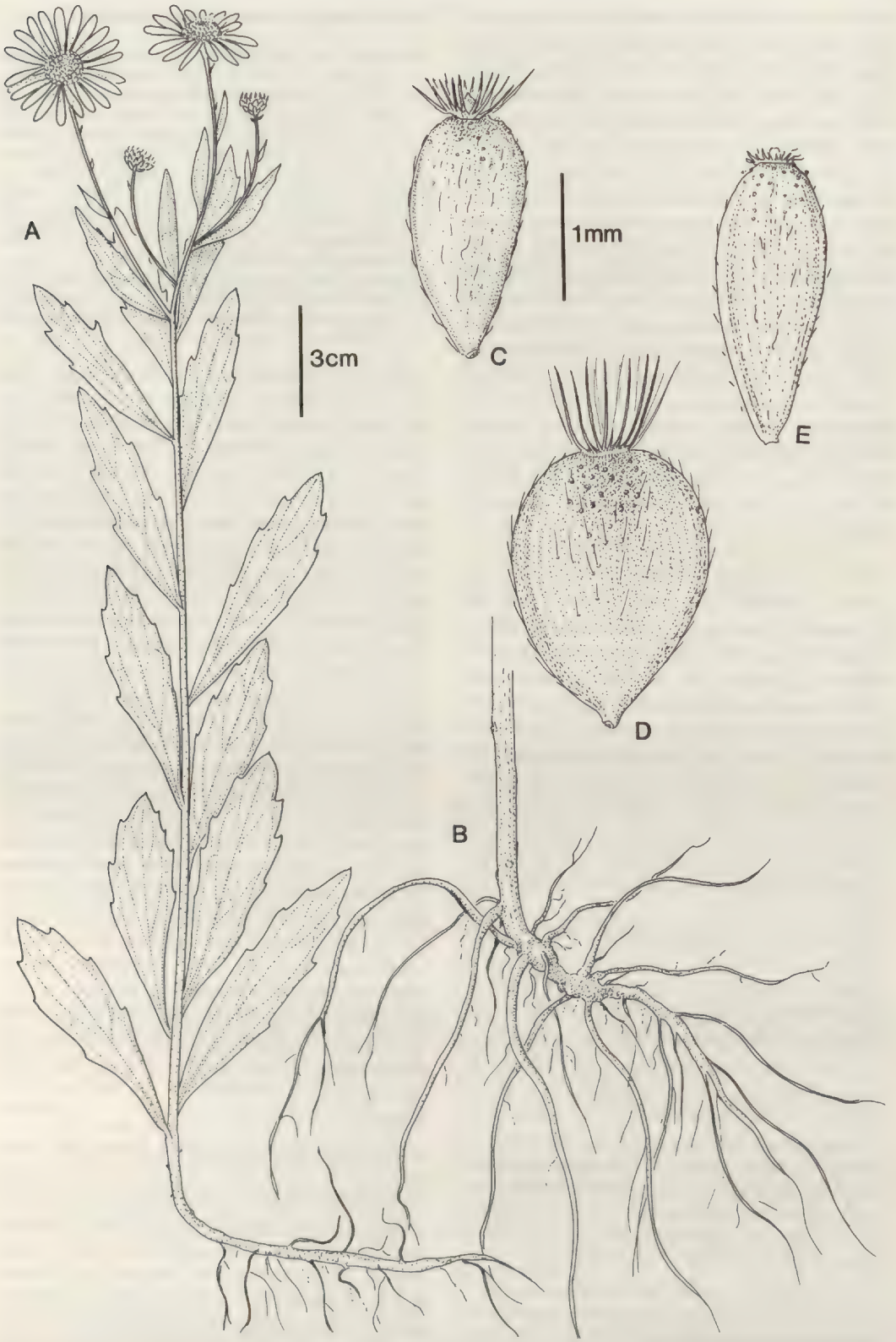
A
3cm
C
1mm
E
D
B

Figure 18. Geographical distribution of *Kalimeris yomena* subsp. *yomena*.

and has been recorded in the Ryukyu Islands (Hatusima, 1975). This taxon grows from sea level to 500 m elevation, usually in relatively sunny and mesic areas frequently disturbed by human activities.

Individuals in areas heavily disturbed by human activities often resprout from cut stems or rhizomes, usually resulting in plants with shorter branches and bigger leaves. One such specimen from Hyogo, *M. Togashi s.n.*, 25 Nov. 1965 (A, TI), is unusual in having an almost creeping stem, bigger leaves and achenes than usual, and later flowering time.

Kalimeris yomena subsp. *yomena* is very common and occurs sympatrically with subspecies *dentata* in Kanto and northern Kinki Districts. Some populations of these two subspecies grow so close together that duplicate specimens contain both taxa. For example, *K. Okamoto 690* from Tokyo has been distributed to several herbaria; those deposited at MO and NY are subspecies *yomena*, whereas those at A, BM, K, KYO, TI, and TNS are subspecies *dentata*. Subspecies *yomena* and *angustifolia* often grow sympatrically, as well, and intermediates commonly occur in the sympatric zones.

Additional specimens examined. JAPAN. **Miyagi:** Watari Gun, "Yukiana," *Saito s.n.* (KYO). **Chiba:** Funabashi Shi, Komuro-cho, *Ohba 652000* (K); Matsudo Shi, *Okuyama s.n.* (TNS). **Saitama:** Minamisaitama Gun, Shiraoka-cho, Ohyamamura, *Ehara 48* (MAK); Urawashi Shi, Tajimagahara, *Murata & Togashi 4* (KYO). **Tokyo To:** Hino Shi, Tamagawahara, *Makino s.n.* (MAK); Katsushika-ku, Mizumoto to Koaidame, *Ohba 61101* (TI); Meguro-ku, Komaba, *Muramatsu s.n.* (TI); Mt. Osawa, Koshigaya, *Ohwi 1002* (K); "Shiwasuda-machi," *Okamoto 690* (MO, NY), *Terasaki s.n.* (K); Suginami-ku, Kugayama, *Yamatsuta 4299* (TNS); Tama Gun, Mt. Mitake, *Furusawa s.n.* (TI); Tama Shi, Sekido, *Okuyama s.n.* (TNS). **Kanagawa:** Yokohama Shi, Kamishirane, *Takahashi s.n.* (MAK), *Maximowicz s.n.* (BM, G, GH, NY), *Milne s.n.* (BM); Zushi Shi, Mt. Jinmuji, *Makino s.n.* (MAK); Mt. Shinmujisan, *Makino s.n.* (MAK), *Okuyama 17476* (TNS). **Niigata:** Kashiwazaki Shi, *Abe s.n.* (MAK); Minamikan Gun, *Shigeru 200* (KYO); Nishikanbara Gun, Ajigata-mura, *Kurihara 99* (MAK); Takata Shi, Minamishiro, *Junkan s.n.* (KYO); Tsubame Shi, Tsubakuro, *Eguchi s.n.* (TI). **Toyama:** Nakaniikawa Gun, Kamiichi-cho, Oiwagawa, *Kurosaki 2607* (TNS). **Nagano:** Kiso Gun, Yamaguchimura, *Oda s.n.* (KYO); Matsumoto Shi, *Koidzumi 27236* (TNS), *65094* (TNS). **Shizuoka:** Ihara Gun, Fujigawa-cho, Arinase River 150–350 m, *Tateishi et al. 4496* (TI); Kamo Gun, Kawazu-cho, Mineyama, 200 m, *Inoue & Im 2252* (TI); Ogasa Gun, Ogasayama, *Sato s.n.* (MAK). **Aichi:** Toyohashi Shi, *Torii 2392* (KYO); Toyokawa Shi, Mikami, *Torii s.n.* (TNS). **Gifu:** Gifu Shi, *Shiota s.n.* (TNS); Toki Shi, Tsumaki, *Shiota*

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Figure 17. *Kalimeris yomena*. A–C. *K. yomena* subsp. *yomena*. —A. Shoot. —B. Root. —C. Achene. —D. Achene of *K. yomena* subsp. *angustifolia*. —E. Achene of *K. yomena* subsp. *dentata*.

8134 (GH). **Ishikawa:** Fugeshi Gun, Monzen-cho, *Kitamura s.n.* (KYO). **Fukui:** Nanjo Gun, Kono mura, Jindo, 150–250 m, *Kurosaki 11017* (KYO); Yoshida Gun, Eiheiji-cho, Daibutsujiyama, *Murata 14327* (KYO). **Shiga:** Kamo Gun, Uchiike, *Hashimoto 754* (A, G, GH, KYO, TI); Kashima Shi, *Baba 11* (KYO); Kusatsu Shi, *Hashimoto s.n.* (KYO); Ohtsu Shi, *Sono s.n.* (TNS). **Mie:** Ichisi Gun, Misugi-mura, between Hirakura and Kawakami, 400–500 m, *Murata 18437* (KYO); Watarai Gun, Hohara, *Suzuki s.n.* (KYO). **Nara:** Ikoma Gun, Mt. Ikomayama, Kuragaritoge, 350 m, *Murata 19662* (A, E, KYO, MAK, MO, NY, TI, TNS); Uda Gun, Haibara-cho, *10069* (TI). **Wakayama:** Naga Gun, Kokawa-cho, Kasukami, Mt. Ryumon-zan, *Ogawa s.n.* (KYO). **Osaka:** Ibaraki Shi, *Beattie & Kurihara 11205* (GH); Mt. Katsuragi, *Kitamura s.n.* (KYO). **Kyoto:** Ayabe Shi, from Ohbatake to Iden, 50–100 m, *Mimoro et al. 4008* (KYO); Fukuchiyama Shi, *Aracki s.n.* (KYO); Kasa Gun, Ooe-cho, Naigu, *Murata 20083* (KYO); Kyoto Shi, Fushimi-ku, Kanaido, 10 m, *Kazumi Tsuchiya 2121* (KYO, TI); Minami-ku, Kameoka, *Hiroe 6441* (TNS); Sakyo-ku, Mt. Hiei, *Makino s.n.* (MAK), *Okamoto s.n.* (TNS); Ohhara, *H. Gu et al. 412* (MO); Tanaka, Higashitakahara, *Kitamura s.n.* (KYO); Shinkotari, *Yamamoto 384* (KYO); Ukyu-ku, Arashiyama, *Kitamura s.n.* (KYO); Mukou Shi, *Yamamoto 3446* (TI, TNS); Otokuni Gun, Shikoutari-mura, Shoryuji, *384* (TNS), *386* (TI); Tsuzuki Gun, Tanabe-tyo, *Murata 8355* (KYO). **Hyogo:** Aioi Shi, Futatsugi to Yado through Tsubakitoge, 50–140 m, *Fukuoka et al. 994* (KYO); Akashi Shi, Ohkubo-cho, 20 m, *Kurosaki 13994* (KYO); Akou Gun, Kamigoori-cho, Yaho, Kaisaka, 150–250 m, *Kurosaki & Kato 148* (KYO); Himeji Shi, Matogatamura, *Togashi s.n.* (A, TI); Kakogawa Shi, Ranno-cho, Saijou, *Kurosaki 9716* (KYO); Hanma, *Makino s.n.* (MAK); Kobe Shi, Hanayama, 200 m, *H. Gu & Noguchi 425* (MO); Hutatabidani, *Okamoto 19678* (TI); Fukuji, Hachiman-jinya, 180 m, *Fukuoka 9887* (KYO); Naka, 50 m, *H. Gu & Noguchi 424* (MO); Miki Shi, Masuda, 150 m, *421* (MO); Nakasato, 90 m, *422* (MO); Ronhayama, 200 m, *423* (MO); Tose, *418* (MO); Sanda Shi, Aimoto, Mt. Kokuzosan, 200–400 m, *Kurosaki 6542* (KYO); Takasago Shi, Iho-cho, *11585* (KYO); Taki Gun, Sasayama-cho, Okugawa, Ohno-yama, *Saimi 5857* (KYO), *Tagawa 6748* (KYO); Tsuna Gun, Hokutan-cho, Nojima, 20–260 m, *Kurosaki 13656* (KYO), *Arimoto s.n.* (GH). **Okayama:** Atetu Gun, Tetta-cho, Kawanose to Takaino, *Kurosaki 14560* (KYO); Okayama Shi, *Nishihara s.n.* (TNS); Takahashi Shi, Deguchi, *Yoshino s.n.* (KYO, TI). **Tottori:** Tottori Shi, *Tanaka 13885* (KYO). **Hiroshima:** Aki Gun, Kabe, Mizuochi, *Shimotomai s.n.* (KYO); Nakahara, Nenoyakawa, *Shimotomai s.n.* (KYO); Nakahara, Uehara, *Shimotomai s.n.* (KYO); Hiroshima Shi, Asakita-ku, 100–120 m, *H. Gu et al. 383* (MO), *384* (MO), *385* (MO); Aburagi, 250 m, *382* (MO); Eba, *Suzuki s.n.* (MAK); Saeki Gun, Yoshiwa-mura, Ishihara, 500 m, *H. Gu et al. 381* (MO). **Shimane:** Hinokawa Gun, Kunitomi-mura, *Hara s.n.* (TNS), Hayashigi to Gakuenji, *Kishino s.n.* (KYO); Mt. Sanbei, *Kitamura s.n.* (KYO); Yatsuka Gun, Shimane-mura, Takohana, *Okuyama & Utsumi 11470* (TNS). **Yamaguchi:** Abu Gun, Atou-cho, Ikumo, *Oka 34250* (TNS), Chomonkyo, Yunose to Akagane, *Murata et al. 126* (KYO), Ikumonaka, 280 m, *H. Gu et al. 377* (MO); Iwakuni Shi, Shiniwakuni, Hakusan Shrine, 14 m, *Charette 1454* (MO); Ootsu Gun, Hiki-cho, *Oka 6496* (KYO), *6497* (TNS); Ohtsu-shima, Tokuyama, *Okamoto s.n.* (KYO, TNS); Saba Gun, Tokuji-cho, Kamimura, *Sato s.n.* (TI), Wado-mura, Tsuuraketoge, *Migo s.n.* (KYO); Shimonoseki Shi, Ayaragi, *H. Gu et al. 371* (MO), *371a* (MO); Tokoura Gun, Houhoku-cho, Kurino-toge, *373* (MO), Nagatoawano, *374* (MO); Tsuno Gun, Kano-cho, *Okuyama 18011* (TNS); Yoshiki Gun, Ogoori-cho, *Oka 3647* (KYO, TNS). **Kagawa:** Kagawa Gun, Shiyoe-cho, Kaharashimo, *H. Gu & Takahashi 386* (MO); Mitoyo Gun, Toyohama-cho, Shirai-toge, *406* (MO); Ohkawa Gun, Hiketa-cho, 200 m, *Takahashi 1702* (KYO, TI); Takamatsu Shi, Taisanji, *H. Gu & Takahashi 402* (MO); Tosannishi, *410* (MO). **Tokushima:** Kaifu Gun, Shishikui-cho, *Takato 311* (KYO); Myodo Gun, *Nakai 2534* (TI). **Kochi:** Kami Gun, Noichi-cho, *Yamanaka 54349* (KYO); Ikku, *Yanagida s.n.* (KYO), *Makino s.n.* (MAK); Takaoka Gun, Sakawa-cho, *Makino s.n.* (MAK); Tosa Gun, Tosayama-mura, *Okubo s.n.* (KYO); Kuwao, *Yamanaka 26157* (KYO). **Ehime:** Higashiuwa Gun, Uwa-cho, Iwaki, *Nomura 3* (KYO); Kamiukena Gun, Mikawa-mura, Nanatori, 500 m, *H. Gu & Takahashi 398* (MO); Matsuyama Shi, Ishitegawa, *Furusawa s.n.* (TI); Sairinji, *H. Gu & Takahashi 400* (MO); 2 km N of Matsuyama Harbor, *403* (MO), *Makino 44* (MAK); Nishiuwa Gun, Ikata-cho, Minatoura, *Nomura s.n.* (KYO); Oshu Shi, *Asayama s.n.* (TNS); Shuso Gun, Takasu, *Yogo 3557* (TNS); Tanbara-cho, Tanogamikada, 310 m, *H. Gu & Takahashi 404* (MO). **Fukuoka Province:** Fukuoka Shi, Mt. Aburayama, *Momiyama s.n.* (TI); pharmacy college, *Nakashima 16552* (TNS); Minami-ku, Heiwa, 10 m, *Tsutsui 27260* (KYO); 165 m, *Tsutsui 27532* (KYO), Nishi-ku, Otoishi, 60 m, *25505* (KYO); Itoshima Gun, Shima-mura, Koganemaru, *Doki s.n.* (KYO); Kikuhantou, Moji-ku, *Hashimoto s.n.* (TI); Nakayawa, *Yoshioka 12* (KYO); Kyoto Gun, Karita-cho, Oazatsutsumi, 200 m, *H. Gu et al. 370* (MO); Tagawa Shi, *Oouchi & Okuyama 20385* (TNS); Yukuhashi Shi, Kawashima, *H. Gu et al. 368* (MO). **Saga:** Hikosan, *Kitamura s.n.* (KYO); Iki Gun, Nakamura-shi, Sumiyoshi, *Hiroe 5120* (KYO); Nagasaki Shi, Mt. Inasayama, *Yamasaki s.n.* (TI); Mt. Tara, *Kitamura s.n.* (KYO). **Nagasaki:** Fukuejuma, Minamimatuura Gun, Koumu, *Fukuoka 11801* (KYO); Tamauoura-cho, Arakawa, *Murata & Koyama 44480* (KYO); Higashisonogi Gun, Kawatana-cho, *Toyama s.n.* (TNS); Kimimashiki Gun, Kousa-cho, *Shimada 13019* (KYO); Matsura Gun, Minamitahira-mura, *Tashiro s.n.* (TNS); Nishisonogi Gun, Tarami-cho, Funazu, *Murata 8415* (KYO, TI); Ohmura Shi, *Toyama s.n.* (TNS); Tsushima, Iki Gun, Naka-mura, Samiyoshi, *Hiroe 5113* (KYO), *Yabe s.n.* (TI). **Kumamoto:** Kikuchi Gun, Otsu-cho,Yatsushiro to Mt. Aso, *H. Gu et al. 357a* (MO); Tara Mts., Kurogi, *Hara s.n.* (TI); Yatsushiro Shi, *Mayebara 5800* (KYO, TNS). **Oita:** Beppu Shi, Otohara, *Murata 12631* (KYO); Oita Shi, Haneya, *Shimada 12991* (KYO). **Miyazaki:** Higashiusuki Gun, Katogawa-cho, *Nakasawa s.n.* (TNS); Hosojima, *Kitamura s.n.* (KYO); Hyuga Shi, *Nagasawa s.n.* (TNS). **Kagoshima:** Hiki Gun, Fukiage-cho, Otomezuki, *H. Gu et al. 349* (MO); Kagoshima Shi, Shiroyama, *Murata 12681* (KYO); Kawanabe Gun, Botsu-cho, Minegasaki, *Furuse s.n.* (A); Oouro-cho, Mt. Isomayama, 300 m, *H. Gu et al. 350* (MO), *351* (MO), *352* (MO); Ibusuki Gun, *Hatusima & Sako 27950* (MAK); Kiire-cho, *Makino s.n.* (MAK); Kaseda Shi, SE of Mt. Isoma, 200–350 m, *Ohba & Akiyama 2559* (TI); Kimotsuki Gun, Sata-cho, Odomari to Sotonoura, 100 m, *Yamazaki et al. 425* (TI); Kitamorogata Gun, Miike, 350 m, *Koyama 7541* (KYO); Kumage Gun, Kamiyaku-cho, Kusukawa, *Oka 37697* (TNS); Satsuma Gun, Tougou-cho, *Doi 40* (KYO); Taromizu Shi, Shinmidoo, Kamishinmidoo to Horikiri, 50–500 m, *Murata 114890* (TI); Yakushima, from Miyanoura to Shitoko, *Iwatsuki 3486* (KYO).

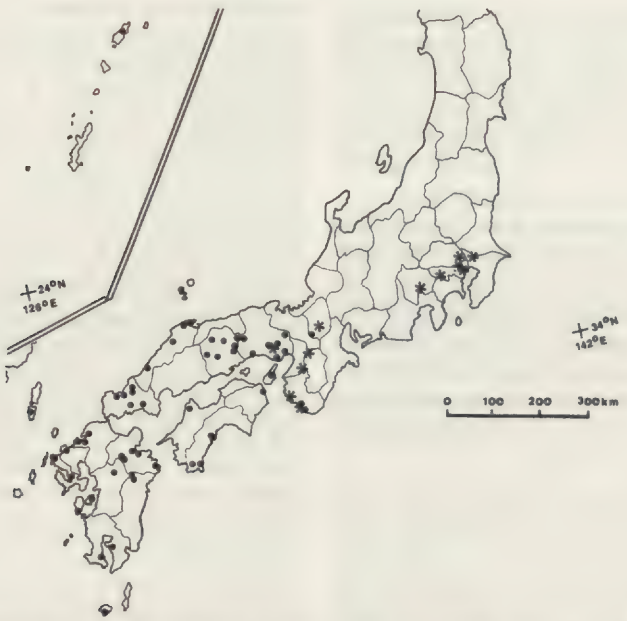

Figure 19. Geographical distribution of *Kalimeris yomena* subsp. *angustifolia* (dots) and subsp. *dentata* (stars).

5b. Kalimeris yomena subsp. **angustifolia** (Nakai) H. Y. Gu, stat. et comb. nov. *Kalimeris pinnatifida* var. *angustifolia* Nakai, Bull. Natl. Sci. Mus. Tokyo 33: 26. 1953. TYPE: Japan. Yamaguchi: Abu-gun, Jifuku-mura, Mt. Ookuraga-dake, 16 Oct. 1949, *T. Nakai & N. Maruyama s.n.* (lectotype, here designated, TNS, 2 sheets; isolectotype, TI).

Rhizomes stoloniferous, 5–30 cm long. Stem green, 70–180 cm tall; branches usually flexible. Cauline leaves narrowly oblong to oblanceolate, serrate, crenate, or deeply pinnate-lobed, 3.5–8.2 × 1.1–2.8(–3.4) cm, glabrous or rarely with scattered, thick, nonglandular hairs adaxially, loosely covered with thick nonglandular hairs and glandular hairs or rarely glabrous abaxially, lobes 0.6–1.5 × 0.3–0.6 cm. Capitula 40–105; peduncles 1.9–9 cm long; bracts 2–13 along the peduncle, the lower ones 7.8–17(–21) × 1.8–2.5 mm, the upper ones 2.5–5.5 × 0.4–0.9 mm; involucre 4.7–8.5 mm broad, 4.2–7.5 mm high. Phyllaries in 3–4 whorls, loosely or tightly imbricate; those of the outermost whorl 2.4–3.6 × 0.8–1.7 mm, those of the middle whorl(s) oblong or obovate, 3.4–5 × 1–2 mm, those of the inner whorl 4–5 × 1–2.1 mm. Receptacles 1.3–2.2 mm wide, 0.6–1.3 mm high. Ray florets 14–22; corollas pale lilac or lilac, ligules 11–17.5 × 2.1–3.5 mm, the tube 1–1.6 mm long; style 2–3.4 mm long, the branches 0.6–1.2 mm long. Disc florets 42–82; corollas 3.2–4.5(–5.1) mm long, the lobes subequal, the longer one 1.2–1.8(–2.1) mm long, the shorter ones 1–1.5 mm long, both 0.4–0.6(–0.7) mm wide, the tube 0.8–1.4(–1.7) mm long; anther 1.1–1.5 mm long; style 2.7–4.4 mm long, the branches 0.9–1.3 mm long. Ray and disc pappus bristles subequal or unequal; ray bristles (0–)0.2–0.5(–0.8) mm long; disc bristles 0.6–0.8(–1.5) mm long. Achenes brownish or purple; margin 0.2–0.3 mm broad; ray achenes 3(–4)-ribbed, 2.2–3 × 0.8–1.4(–1.9) mm; disc achenes 2-ribbed, 2.8–3.5 × 1.4–2.3 mm. Chromosome number: $2n = 66$, 68, 69, 70, 71, 72, 73. Figure 17D.

Phenology. Flowering period: June to late October.

Distribution (Fig. 19). Endemic to Japan, from southern Honshu (from Shiga and Hyogo prefectures south and west; also on Oki Island), Shikoku, and Kyushu, to Yaku Island. It occurs predominantly at low elevations, but is also found as high as 1200 m. Like other taxa of the genus, *K. yomena* subsp. *angustifolia* generally occurs in sunny, relatively mesic places, often around human disturbance. It is sympatric with *K. indica* subsp. *indica* in southern Kyushu and with *K. yomena* subsp. *yomena* in most parts of its distributional range.

Kalimeris yomena subsp. *angustifolia* has long been called *K. incisa* in taxonomic treatments by Japanese botanists (e.g., Kitamura, 1937b; Ohwi, 1965; Ito & Soejima, 1995, as *Aster incisus*). The confusion has been caused mostly by its longer pap-

pi, which also characterize *K. incisa*. These two taxa differ, however, in branching pattern and rhizome morphology, with *K. yomena* subsp. *angustifolia* having flexible branches up to 40 cm long and stoloniferous rhizomes up to 10 cm long, whereas *K. incisa* has relatively stiff branches less than 25 cm long and condensed rhizomes no longer than 1 cm.

There are two morphological forms found in this subspecies: one with relatively narrow leaves and phyllaries, and the other with broader leaves and phyllaries. These two forms are not allopatric, nor do they exhibit any habitat preferences. There are no other character states correlated with these two forms. Intermediates between them are often found in the herbarium as well as in the field. They are here treated as a single taxon.

Additional specimens examined. JAPAN. **Shiga:** Gamou Gun, Kitahizusa-mura, Uchiike, *Hashimoto 13500* (TNS); Ohtsu Shi, Hishigakaro, *4714* (TNS). **Wakayama:** Nishimuro Gun, Hikigawa-cho, *Fukuda s.n.* (TI); Inarimura, *Nakajima s.n.* (TI); Tanabu Shi, *Nakajima s.n.* (TI). **Osaka Fu:** Kongo-san, Chihaya to Fushimi-toge, 500 m, *Murata 19038* (KYO), *Tada s.n.* (TI). **Kyoto:** *Makino s.n.* (MAK). **Hyogo:** Aku Shi, Nishiune, Kamikumi, Sakaorike, 60 m, *Kurosaki & Kato 22* (KYO); Ibo Gun, Mitsucho, Murotsu, 20–100 m, *Fukuoka 12298* (KYO); Kasai Shi, Aonogahara-cho, Enshujo, 90 m, *Kurosaki 9537* (KYO); Kobe Shi, Hutatabidani, *Okamoto 19677* (TI); Tarumi-ku, *Kitamura s.n.* (KYO), *Makino s.n.* (MAK); Mikata Gun, Hanasaka-cho, Kannon-yama, 50–150 m, *Murata 46619* (KYO); Miki Shi, Ohmura, *Murata & Nishimura 270* (KYO); Minou Gun, Yoshikawa-cho, Hase, 85 m, *H. Gu & Noguchi 420* (MO); Sanda Shi, Mt. Kokuzosan, Aimoto, *Kurosaki 6542* (TI); Shisou Gun, Chikusa-cho, *Utsumi s.n.* (KYO); Sumoto Shi, in Awaji-shima, Yura-cho, Narugashima, *Kurosaki et al. 2705* (KYO); Takenokuchihachimanjinjya, 0–50 m, *Fukuoka et al. 2664* (KYO); Takasago Shi, Ooishi, Ishinohoden, 20–60 m, *Kurosaki 12928* (KYO); Umei, at sea level, *140001* (KYO); Taki Gun, Sasayama-cho, *Araki s.n.* (KYO), *Saimami s.n. in 9/1968* (KYO). **Okayama:** Aida Gun, Awakura-mura, Shiotani, *Nanba 8160* (KYO, TNS); Akayama Gun, *Uno 94* (NY); Atetsu Gun, along Nisikawa, Hubara, Kamiitikyo, *Tagawa s.n.* (KYO); Mt. Iwayayama, *Hara & Kurosawa s.n.* (TI); Mimi Shi, Sakamoto, Kosehara, 350 m, *Fukuoka 11250* (KYO); Nohara, *Nishihara s.n.* (TNS); Niimi Shi, Ikura, *Hara & Kurosawa s.n.* (TI), *Tashiro s.n.* (KYO). **Hiroshima:** Asa Gun, Fukuda-mura, Fukuugi, Terawake III, *Shimotomai s.n.* (KYO); Jinseki Gun, Yuukicho, Senyoo, *Tashiro s.n.* (TNS); Hiroshima Shi, Ushitamura, *Suzuki s.n.* (KYO); Mt. Micoto, *Tashiro s.n.* (KYO); Takada Gun, Mukaihara, Mt. Otsuchi, *Terabayashi 728* (KYO), *Kuriyama 2009* (MAK). **Shimane:** Hirata Shi, Jurokujima, *Miyamoto 80* (MAK); Naga Gun, Mishumi-cho, *Saito 270* (MAK); Nima Gun, Yunotsu-cho, Matsuyama, *Takaki 327* (KYO), Yunotsu, sea coast, *Miyamoto 105* (MAK); Mt. Sanbusan, *Maruyama 512* (TNS); Shimazenshima, Koniga, *924* (KYO), *925* (KYO); Mt. Tainosu, *Kitamura s.n.* (KYO). **Yamaguchi:** Abu Gun, Ato-cho, Chomonkyo, between Yunose and Akagane, *Murata et al. 128* (KYO); Jifuku-mura, Mt. Ookuraga-dake, *Oka 3671* (TI); Hagi Shi, Kasayama, *22925* (KYO), *Kiatsu s.n.* (KYO); Ohtsu Gun, Mt. Ichiigadake, *Hiroe 5071* (KYO); Ohtsu Gun, Hiki-cho, Ohuchiyama, *H. Gu et al. 375* (MO); Shimonoseki Shi, Umegatou, *372* (MO); Tokuyama Shi, Kyoto University, *Okamoto s.n.* (KYO, TNS); Tsuno Gun, Kanocho, Okeyama, 500 m, *H. Gu et al. 379* (MO); Yamaguchi Shi, *Oka 3671* (TI). **Kagawa:** Mitoyo Gun, Yamamotocho, Nitta, *H. Gu & Takahashi 407* (MO); Nakatado Gun, Kotohira-cho, Sabun, 360 m, *408* (MO); Takamatsu Shi, Yashima, *411* (MO). **Tokushima:** along Katsuurakawa, *Murai 33* (KYO). **Kochi:** Iwata Gun, Saga-cho, Iyoki, *Murata 6682* (TI), *6692* (TI); Kami Gun, Noichi-cho, from Shinmiya to Nishino, *H. Gu & Takahashi 395* (MO); Tosayamada-cho, Kageyama, 240 m, *393* (MO); Koch Shi, Godaiyama, 100 m, *397* (MO); Ushioe-yama, *Makino s.n.* (MAK); Mima Gun, Waki-cho, Nakayamagi, *H. Gu & Takahashi 389* (MO); Nangoku Shi, Ueda, *392* (MO); Shukumo Shi, Kozukushi, *Murata 6864* (TI); Shusaki Shi, Toshima, *Makino s.n.* (MAK). **Ehime:** Matsuyama Shi, Sairinji, *H. Gu & Takahashi 401* (MO), *Okuhira s.n.* (MAK), Uma Gun, Doi-cho, Nakamura, *H. Gu & Takahashi 405* (MO). **Fukuoka:** Fukuoka Shi, Tashima, *Nakajima 15499* (TNS); Itoshima Gun, Shima-cho, Keya, *Tashiro s.n.* (KYO); Kashuya Gun, Hisayama-cho, *Nakajima 86* (TNS), *10998* (KYO); Kyoto Gun, Karita-cho, Oazatsutsumi, 200 m, *H. Gu et al. 370a* (MO); Yukuhashi Shi, Kanaya, *367* (MO); Kawashima, *369* (MO). **Saga:** Higashimatsuura Gun, Genkai-cho, Mt. Tensan, *Baba 6* (KYO, TI); Saga Gun, Fuji-cho, Sugiyama, *7* (KYO). **Nagasaki:** Kitamatsuura Gun, Tabira-cho, *Tashiro s.n.* (KYO); Ohmura Shi, *Toyama & Okuyama 18770a* (TNS); Shimoagata Gun, Mitsushima-cho, Sumo, *Momora 1862* (KYO); Tsushima, Shimoagata Gun, 300–400 m, *Koyama 2979* (TNS), *Hara s.n.* (KYO), *Yabe s.n.* (TI), *Oldham 399* (K, W). **Kumamoto:** Amakusa Gun, Amakusakamijima, Ohtsu, *Yamasaki s.n.* (TI); Amakusashimojima, Ushizu Shi, *Makino s.n.* (MAK); Aso Gun, Aso-cho, Muta, *Kitamura s.n.* (KYO); Narukawa, *Hara s.n.* (TI); Ishinomiyacho, Mt. Aso, 1200 m, *H. Gu et al. 359a* (MO), *360* (MO), 1300 m, *363* (MO); Kamimashiki Gun, Yabe-cho, Naidaijin-yama, *Tashiro s.n.* (KYO); Kikuchi Gun, Otsu-cho, Road #57 to Mt. Aso, 450 m, *H. Gu et al. 356* (MO); Yatsushiro Gun, Ryuhoku-cho, Yoshimoto, *355* (MO); Yatsushiro Shi, *Shimada 12993* (KYO). **Oita:** Mt. Aso, Shenchomuda, *Tashiro s.n.* (KYO); Beppu Shi, Inonoseto, *Kokano 8* (KYO), *19* (KYO); Hayami Gun, Nakayamaga, *Tashiro s.n.* (KYO); Mt. Kujyu, *Tashiro s.n.* (KYO); Jijohara, *Tashiro s.n.* (KYO); Kijimabaru, *Tashiro s.n.* (KYO); Mt. Kujyu, *Makino s.n.* (MAK); Kusu Gun, Handamura, Shendomuda, *Tashiro s.n.* (KYO); Yoshibe, Tano, *Tashiro s.n.* (KYO, TNS); Minamiamabu Gun, Tsurumi-cho, *Tashiro s.n.* (KYO); Naoili Gun, Kujiu-cho, Kuninomura, *Makino s.n.* (MAK); Oita Gun, Yuhuin-cho, Yuhuin, Yuhuin hot spring, 700 m, *H. Gu et al. 365* (MO); Oita Shi, Mt. Takasaki-yama, *Tashiro s.n.* (KYO); Mt. Sobosan, *Tashiro s.n.* (TNS). **Miyasaki:** Nishiusuki Gun, Takachiha-cho, *Tashiro s.n.* (KYO, TNS); Kushima Shi, Makaya, 110 m, *Koyama 7550* (KYO); Mt. Sobosan, Gokase plain, *Nagasawa s.n.* (TNS). **Kagoshima:** Hiki Gun, Fukiage-cho, Isaku-toge, 300 m, *H. Gu et al. 348* (MO); Ibushuki Gun, Kiire-cho, *Makino s.n.* (MAK); Ibusuki Shi, *Hatusima & Sako 27950* (MAK); Kaseda Shi, Ayukawa, 70 m, *H. Gu et al. 353* (MO); Kimotsuki Gun, Sata-cho, Odomari to Sotonoura, 110 m, *Yamazaki et al. 425* (TI); Kushikino Shi, *H. Gu et al. 354b* (MO), *354c* (MO), *354d* (MO); Naze Shi, Ohshima, *Kimura & Furusawa s.n.* (TI); Yakushima, Kumaba Gun, Kamiyaku-cho, *Oka 37697* (KYO); Sambon to Sugi, along Kusukawa, 200–600 m, *Murata et al. 15419* (TI).

5c. Kalimeris yomena subsp. **dentata** (Kitam.) H. Y. Gu, stat. et comb. nov. *Kalimeris pinnatifida* var. *dentata* Kitam., Mem. Coll. Sci. Kyoto Imp. Univ., Ser. B, Biol. 13: 309. 1937. *Kalimeris pseudo-yomena* Kitam., Mem. Coll. Sci. Kyoto Univ., Ser. B. 24: 53. 1957, nom. illeg. TYPE: Japan. Kanagawa: Jinmuji, 3 Nov. 1935, *S. Kitamura s.n.* (holotype, KYO; isotype, KYO).

Rhizomes stoloniferous, 5–14 cm long. Stem 50–80 cm tall; branches usually stiff. Cauline leaves linearly oblong, oblong, or oblanceolate, serrate, 4.8–7(–8.6) × 1.1–1.8(–2) cm, covered with thick nonglandular hairs on both sides. Capitula 10–64; peduncles 1.8–7.5 cm long; bracts 2–8 along the peduncle, the lower ones 8.6–19 × 1.5–2.8 mm, the upper ones (1.3–)2.1–7 × 0.4–1.5 mm; involucre hemispherical, 5.5–8 mm broad, 3.5–5.5 mm high. Phyllaries in 3 whorls, those of the outermost whorl 2.2–3.5 × 0.7–1 mm, those of the middle whorl 3.5–5 × 1.1–1.5(–2) mm, those of the inner whorl 3.5–5 × 1–1.7 mm. Receptacles 1.1–1.9 mm wide, 0.5–1.3 mm high. Ray florets 14–22; corollas pale lilac or whitish, ligules 6–14.5 × (1.3–)1.5–2.8 mm, the tube 1–1.7 mm long; style 2–2.6 mm long, the branches 0.6–1.2 mm long. Disc florets 42–70; corollas 3–4.7 mm long, the lobes subequal, the longer one 1–1.5 mm long, the shorter ones 0.8–1.3 mm long, both 0.4–0.6 mm wide, the tube 1–1.4(–1.7) mm long; anther 0.8–1.5 mm long; style 2.4–3.2 mm long, the branches 0.8–1.2 mm long. Ray and disc pappus bristles subequal, 0.2–0.3 mm long. Achenes straw-colored or brownish, the margins 0.1–0.2 mm broad; ray achenes 3(–4)-ribbed, 2.1–2.5 × 0.8–1.1 mm; disc achenes 2(–3)-ribbed, 2.2–3 × 0.8–1.3 mm. Chromosome number: $2n = 40, 41, 43, 45$. Figure 17E.

Phenology. Flowering period: June to late October.

Distribution (Fig. 18). Endemic to Japan, where it occurs in two disjunct areas: Chiba, Tokyo, and Kanagawa prefectures of southeastern Kanto District, and Yamanashi Prefecture of northeastern Chubu District; and to the southwest in Shiga, Nara, Osaka, and Wakayama prefectures of Kinki District. It occurs from near sea level to 850 m elevation and, like the other two subspecies, occurs in similarly disturbed, open habitats. It overlaps in range with both other subspecies, but is less common than either.

Kalimeris yomena subsp. *dentata* is variable both morphologically and cytologically. Judging from the morphology and chromosome numbers, this subspecies might have originated as a hybrid between *K. pinnatifida* ($n = 9$) and an octoploid *K. yomena* subsp. *angustifolia* or subsp. *yomena* ($n = 36$). The three subspecies differ mainly in branching pattern and the morphology of achenes and pappi (Fig. 17). Intermediate individuals are found in areas of sympatry.

Additional specimens examined. JAPAN. **Chiba:** Higashikatsushika Gun, Abiko-cho, *Murata & Togashi 25* (MAK, TI), *36* (MAK, TI), *38* (KYO, MAK). **Saitama:** Ohmiya Shi, *Okuyama s.n.* (TNS); Urawa Shi, Tajimagahara, *Murata & Togashi 11* (MAK, TI). **Tokyo:** Chuo-ku, Hamarikyu, *Okuyama 23799* (TNS); Hachiouji Shi, Mt. Takaosan, *17580* (TNS); Hatogaya Shi, *Shirai s.n.* (TNS); Kamiitaba Shi, Itabashi-ku, *Makino s.n.* (KYO); Nelima-ku. *Makino s.n.* (MAK); Shibuya-ku, *Makino s.n.* (MAK); Shiwasuda-machi (in Musashi), *Okamoto 690* (A, BM, K, KYO, TI, TNS). **Kyoto To:** Kyoto Shi, Sakyo-ku, Tanaka, *Kitamura s.n.* (KYO). **Hyogo:** Miki Shi, Hosakawa, 50–150 m, *Murata & Nishimuar 293* (KYO, TNS). **Yamanashi:** Fujiyoshida Shi, Sengenjinja, 850 m, *Murata et al. 33871* (KYO); Minamitsuru Gun, Misaka Mts., Oishitoge, *Kanai s.n.* (TI). **Shiga:** Kamo Gun, Uchiike, *Hashimoto 754* (BM, MAK, MO, TNS). **Nara:** Ikona Gun, Mt. Ikomayama, Kuragaritoge, 350 m, *Murata 19662* (TNS). **Wakayama:** Nishimuro Gun, Shirahama-cho, Shirahamaguchi Station, *Takahashi 215* (TNS). **Osaka:** Mt. Kongo-san, Chihaya to Fushimi-toge, 500 m, *Murata 19036* (KYO).

6. Kalimeris shimadai (Kitam.) Kitam., Acta Phytotax. Geobot. 6: 50. 1937. *Asteromoea shimadai* Kitam., Acta Phytotax. Geobot. 2: 37. 1933. *Aster shimadai* (Kitam.) Nemoto, Fl. Japan Suppl. 740. 1936. TYPE: China. Taiwan: Shinchi-ku, Chikunan, Zokyo, 50 m, Dec. 1925, *Y. Shimada 2664 c* (holotype, KYO).

Aster yangtziensis Migo, Bot. Mag. (Tokyo) 56: 300. 1942. TYPE: China. Jiangsu: Nanjing, Zi-jin-shan, 23 July 1940, *H. Migo 60* (holotype, KYO).

Kalimeris shimadai f. *pinnatifida* Kitam., J. Jap. Bot. 19: 341. 1943. TYPE: China. Zhejiang: Putuo, 13 Oct. 1935, *H. Migo 49* (lectotype, here designated, KYO).

Root fibrous; rhizomes condensed, 0.1–1 cm long, usually forming rootstocks. Stem (31–)60–200 cm tall. Rosette and lower cauline leaves covered with long and thin nonglandular hairs. Cauline leaves oblong or oblanceolate, crenate, serrate, or deeply pinnate-lobed, 3.5–7.5 × (0.6–)1–2.7 cm, densely or evenly covered with thin nonglandular hairs on both sides and often interspersed with glandular hairs abaxially, lobes 0.4–1 × 0.2–0.4 cm. Capitula 20–85; peduncle 1.6–9.3 cm long; bracts 1–7 along the peduncle, the lower ones 7–18 × 1.3–3.3 mm, the upper ones 3.1–6.1 × 0.8–1.3 mm; involucre campanulate or rarely hemispherical, 6.5–10 mm broad, 4.6–7.5(–9) mm high. Phyllaries in 3–4 whorls, imbricate, covered with thin nonglandular hairs and sometimes interspersed with glandular hairs; those of the outermost whorl

lanceolate or obovate, (2.2–)3–4.7 × 0.8–1.4(–1.8) mm, those of the middle whorl(s) obovate or spathulate, 3.5–6.2 × 1.2–2(–2.5) mm, those of the inner whorl obovate or spathulate, (3.3–)4–6.2(–7.2) × 1–2(–2.3) mm. Receptacles convex, 2–2.8 mm wide, 0.7–1.5 mm high. Ray florets (11–)14–29; corollas pale lilac or light purple, ligules 13.5–21 × 2–3.5(–4) mm, the tube 1.2–2.2 mm; style 2–3.3 mm long, the branches 0.8–1.4 mm long. Disc florets 48–82; corollas 3.5–5.6 mm long, the lobes unequal, the longer one 1.2–2.2 mm long, the shorter ones 0.4–1.4 mm long, both 0.5–0.7(–0.8) mm wide, the tube 1–2 mm long; anther 1.2–2.2 mm long; style 2.8–4.8 mm long, the branches 1–1.4 mm long, each with a triangular or broadly lanceolate appendage 0.4–0.5 mm long. Ray and disc pappus bristles equal or unequal; the ray bristles 0.3–0.6(–1) mm long; the disc bristles 0.4–0.6(–1) mm long. Achenes light brown or purple, broadly obovate, covered with 4-celled biseriate nonglandular hairs and rarely with glandular hairs at the top, the margins 0.2–0.4 mm broad; ray achenes 3(–4)-ribbed, 2.5–3 × 1.2–1.5 mm; disc achenes 2-ribbed, 3–3.2 × 1.7–2 mm. Chromosome number: $n = 54$. Figure 12G–J.

Phenology. Flowering time: June to late November.

Distribution (Fig. 20). This species is endemic to eastern and central China. It occurs from Shanxi, Shandong, Henan, Shaanxi, and Gansu provinces in the north to Anhui, Jiangsu, Jiangxi, Fujian, and Taiwan in the southeast, and to northwestern Hunan, Hubei, and Sichuan in central and southwestern China. It is distributed from low areas at sea level to elevations up to 2800 m. It is usually found on open slopes, dry, stony areas, or sometimes in relatively mesic habitats.

This taxon is often sympatric with *Kalimeris indica* subspp. *indica* and *stenolepis*, and with *K. integrifolia* in Jiangsu and Hubei. Several populations of *K. shimadai* and *K. indica* subsp. *indica* were found co-occurring in Yichang Xian, Hubei and Nanjing Shi, Jiangsu, but no intermediates between these two taxa were detected from these areas. No intermediates between *K. shimadai* and *K. integrifolia* were found in their areas of sympatry, either. *Kalimeris shimadai* and *K. indica* subsp. *stenolepis* are sympatric in Hubei, where they are usually distributed at different elevations. The former occurs at low elevations, mostly below 1500 m but rarely to 2800 m, whereas the latter is often found at higher elevations, mainly from 500 to 3000 m. *Kalimeris shimadai* is also sympatric with *K. lautureana* subsp. *lautureana* in the Loess Plateau, where the higher elevation phenotypes of these two taxa can be difficult to distinguish. Both tend to have deeply pinnate-lobed or serrated leaves at high elevations, but differ mainly by the length and density of branches, the indumentum, and the size of the phyllaries. *Kalimeris shimadai* is characterized by its narrower phyllaries, and leaves densely covered with thin nonglandular hairs.

This species is very common at the southern part of its range. Plants from Taiwan have relatively broad phyllaries and thin rhizomes with relatively long internodes. Smaller individuals are more characteristic of the northern part of the geographic range. The length of the pappus bristles also varies in this species; usually they are relatively long, with united bases, but epappose individuals are occasionally found (*T. P. Wang 5062*, PE, WUK; and *Tang Sui Ging 5706*, BM, MO).

Additional specimens examined. CHINA. **Shanxi:** Hongdong, *Kanasiro 4838* (KYO); Jiechou (Chieh Hsiu), Songlinmiao, 800 m, *Smith 7677* (A, BM, W); Xiachuan Xian, Yaoshan, 1500 m, *Licent 12506* (W); Xia Xian, Sijiao, Chepuyu, Houliang, 1400 m, *T. W. Liu 749* (PE), 1350 m, *751* (PE); Sijiao, Xigou-dadui, Baicaigou, 1250 m, *697* (PE); "Central Shensi," *Licent 2422* (BM, W). **Shandong:** Jinan Shi, *Shandong University Team s.n.* (GH). **Henan:** Lingbao Xian, Wenyu-cun, Jianziyan, 720 m, *J. Q. Fu 40* (IBSC, WUK); Lushi Xian, Tazi-shan, *Huangtu-gaoyuan Team 1969* (WUK). **Shaanxi:** Feng Xian, Huangniupu, Huji-shan, *Z. Y. Zhang 189* (WUK); Fuping Xian, Houzhenzi-xiang, Damonghe, 1075 m, *X. M. Zhang 332* (HIB); Hu Xian, Beimenwai, *Y. Y. Pai 1282* (PE); Mian Xian, Wuhouchen, *K. T. Fu 3590* (PE, WUK); Ruicheng Xian, Fang-shan, *S. Y. Bao 600* (PE), *1500* (PE), *1586* (PE), *1587* (PE); Shannan Xian, Caoying, Shuangjian, 1500 m, *B. Z. Gou 3996* (PE); Shanyang Xian, Mantou-shan, 1500 m, *T. P. Wang 16313* (PE, WUK); Sixian, Shangtian-shan, 1600 m, *3626* (PE, WUK); Dameiqiao, 1200 m, *2957* (PE, WUK); Taibai-shan, Liujiayan, *W. Y. Hsia 4744* (PE), *4748* (PE); Songpingsi, 1200 m, *T. N. Liu & P. C. Tsoong 75* (PE); Yingtokou, *Y. Y. Pai 1399* (PE, WUK), *T. P. Wang 1436* (PE); Taibai Xian, Guaili-xiang, *620 Team 3-357* (PE); Zhouzhi Xian, 650 m, *H. W. Kung 3737* (PE). **Gansu:** Heshui Xian, Lianjiabian, *Y. H. Sun & Z. S. Jin 252* (PE, WUK); Huicheng Xian, Taihe-gongshe to Fangyan-zhuang, 1400 m, *Z. Y. Zhang 662* (KUN, WUK); Lintan, 2800 m, *T. P. Wang 5062* (PE, WUK); Min Xian, 2600 m, *5045* (PE, WUK); Taoho Xian, Toumenkuan, 2300 m, *5975* (PE, WUK); Zhang Xian, *Huanghe Team s.n.* (PE). **Anhui:** Chao Xian, Dongyan, *Huadong Field Station Team 3776* (PE); Quanjiao Xian, *5475* (PE); Shucheng Xian, Gou'erkou, Hongjiachong, *4488* (PE). **Jiangsu:** Baohua-shan, *Merrill 1526* (K, PE); Danyang Xian, *Nanjing Forestry College Team 7800-746* (IBSC); Jiangpu Xian, Tangquan, Lao-shan, Xiaofulong-shan, 120 m, *F. B. Deng et al. 3726* (KUN); Jiangyin Xian, Hua-shan, 20 m, *H. B. Zhou 3021* (IBSC); Jingjiang Shi, *Kolshaff 95* (W), Zhulinsi, *Migo 42* (KYO); Jurong Xian, Mao-shan, Jinniudong, 120 m, *F. B. Deng et al. 3519* (PE); Kunshan Xian, *Migo 45* (KYO); Nanjing Shi, Zijin-shan, *C. R. Huang s.n.* (TI), *Matsuda s.n.* (TI), *C. C. Chang 4* (E), *C. N. Chen 8621* (W), *C. Y. Chiao*

Figure 20. Geographical distribution of *Kalimeris shimadai*.

14941 (PE), *K. S. Chow 80259* (BM, K, KYO, NY); Suzhou Shi, Shangfang-shan, *K. Ono s.n.* (TI); Yixing Xian, Wufu, *K. Ling 2310* (GH); Zhengjiang Shi, Feng-shan, *Huadong Field Station Team 2974* (KUN). **Jiangxi:** Jiujiang Shi, *Carles 438* (E), *Migo 61* (KYO), *Sheaver s.n.* (GH, K); Lu-shan, *Y. G. Xiong 10070* (PE); Xiajiang Xian, Laoping, *Chavet 804* (W). **Fujian:** Gu-shan, *T. C. Chang 2906* (A), *S. G. Tang 5706* (BM, MO); *Fudan University Team 50531* (KUN), *Z. X. Zhao 890* (KUN). **Taiwan:** Miaoli County, Tung-hsiao, Ping-ting, *Tamura & Koyama 32106* (KYO, TI, TNS). **Hunan:** Xiangsi Zizhiqu, Longshan, Hongyan-cun, 600 m, *L. H. Liu 9357* (PE). **Hubei:** Jiangling Xian, Jiangling, Xiuhu, 20 m, *Q. H. Liu 1073* (HIB); Yichang Xian, Xiaoxita, *H. Gu & D. Chen 183* (MO), *189* (MO), *Henry 2739* (G), *2739a* (K), *Wilson 1727* (K, W); Zaoyang Xian, Pinglin-gongshe, Guanji-dadui, *D. Y. Mu 297* (HIB). **Sichuan:** from Chongqing to Chengdu, *T. N. Liu 9854* (WUK); from Hanyan to Yidong, *X. J. Yang 3625* (PE); Kangding Xian, Feiyueling, 2520 m, *C. S. Liu 1584* (PE).

7. **Kalimeris lautureana** (Debeaux) Kitam., Acta Phytotax. Geobot. 6: 22. 1937. *Boltonia lautureana* Debeaux, Actes Soc. Linn. Bordeaux 31: 215. 1876. *Aster lautureanus* (Debeaux) Franch., Mém. Soc. Sci. Nat. Cherbourg 24: 224. 1884. *Asteromoea lautureana* (Debeaux) Hand.-Mazz., Acta Horti Gothob. 12: 224. 1938. TYPE: China. Shandong: Yantai, 4 July 1860, *O. Debeaux 93* (lectotype, here designated, P).

Root fibrous; rhizomes condensed, usually forming rootstocks. Stem (50–)78–140 cm tall, loosely to densely covered with thin nonglandular hairs. Rosette leaves covered with the same type of hairs as on the stem. Cauline leaves oblong to broadly oblong, entire or deeply lobed, 3.2–7.7 × 0.6–2.4 cm, glabrous or sometimes evenly covered with nonglandular hairs or only so along the veins, lobes 0.4–0.9 × 0.1–0.3 cm. Capitula 10–90; peduncle 1.6–9(–13) mm long; bracts 2–10 along peduncle, the lower ones 6.2–15 × 0.9–4 mm, the upper ones 2.1–6 × 0.5–1 mm; involucre campanulate, rarely hemispherical, 6.5–10 mm broad, (4–)4.8–7(–7.8) mm high. Phyllaries in 3–4 whorls, tightly imbricate, glabrous or covered with nonglandular hairs; those of the outermost whorl lanceolate, oblong, or obovate, (2.3–)2.6–4.5 × 0.8–1.9 mm, those of the middle whorl(s) obovate or less often spathulate, 3.2–5.8(–6.2) × 1.3–2.3(–3) mm, those of the inner whorl obovate to spathulate, 4.7–6.5(–7.6) × (1.4–)1.8–2.5(–3.2) mm. Receptacle convex, 1.6–2.5 mm wide, 0.5–1.8 mm high. Ray florets 13–22; corollas whitish to lilac, ligules 13–28 × 2.5–4(–4.3) mm, the tube 1.4–2.6 mm long; style 2–4.5 mm long, the branches 0.5–1.1(–1.5) mm long. Disc florets 30–95; corollas 4–5.8 mm long, the lobes unequal, the longer one 1.5–2.2 mm long, the shorter ones 0.7–1.6(–1.8) mm long, both 0.5–0.7(–0.8) mm wide, the tube 1–1.8 mm long; anther (1–)1.4–2.1 mm long; style 3–5 mm long, the branches 0.8–1.6 mm long, each with a triangular or broadly lanceolate appendage 0.8–1.6 mm long. Ray and disc pappus bristles straw-colored or brownish, unequal; ray bristles 0.2–0.5(–0.8) mm long; disc bristles 0.4–0.6(–1) mm long. Achene greenish or light purple, obovate to broadly obovate, covered 4-celled nonglandular hairs and rarely scattered with glandular hairs at the top, the margins 0.2–0.4 mm broad; ray achenes 3-ribbed, 2.2–3 × 1.2–2 mm; disc achenes 2-ribbed, 2.4–3 × 1.6–2 mm. Chromosome number: $n = 54$. Figure 21.

Kalimeris lautureana is distributed mostly in east and central China from coastal areas to montane regions. Two subspecies can be recognized, as follows:

KEY TO THE SUBSPECIES OF *KALIMERIS LAUTUREANA*

1a. Leaves oblong, 0.6–2 cm wide; ray florets shorter than 25 mm; phyllaries of the middle whorl(s) to ca. 2.5 mm wide; disc corollas 4–5.1 mm long ..... 7a. subsp. *lautureana*

1b. Leaves broadly oblong, 1.5–2.4 cm wide; ray florets longer than 25 mm; phyllaries of the middle whorls to ca. 3 mm wide; disc corollas 5–5.8 mm long ..... 7b. subsp. *mangtaoensis*

7a. **Kalimeris lautureana** subsp. **lautureana**

Stem 60–140 cm tall. Cauline leaves oblong, rarely oblanceolate, entire to deep-serrate or less often lanceolate-lobed, 3.2–6(–6.9) × 0.6–2 cm, lobes 0.4–0.9 × 0.2–0.3 cm. Capitula 20–90; peduncle (1.6–)2.5–10(–13) cm long; bracts 3–10 along peduncle, the lower ones 6.2–15 × 0.9–2.8 mm wide, the upper ones 2.1–5.6 × 0.5–1 mm; involucre campanulate or less often hemispherical, 6.5–9 mm broad, 4.6–7.5 mm high. Phyllaries in 3–4 whorls; those of the outermost whorl 2.3–4 × 0.8–1.7 mm, those of the middle whorl(s) 3.6–6 × 1.6–2.5 mm, those of the inner whorl 4.8–6.5 × (1.4–)1.8–2.6 mm. Receptacles 1.6–2.5 mm wide, 0.5–1.2 mm high. Ray florets (13–)15–22; ligules (13–)14–22 × 2.7–3.8 mm, the tube 1.4–2(–2.5) mm long; style 2–3.2 mm long, the branches 0.5–1.1 mm long. Disc florets (30–)45–95; corollas 4–5.1 mm long, the lobes unequal, the longer one 1.5–2.2 mm long, the shorter ones 0.9–1.8 mm long, both 0.5–0.7 mm wide, the tube 1–1.7 mm long; anther 1–1.8 mm long; the branches 1–1.5 mm long. Ray and disc pappus bristles unequal; ray bristles 0.2–0.6(–1) mm long; disc bristles 0.4–0.8(–1.5) mm long. Achene straw-colored or light purple; ray achenes 2.2–3 × 1.2–2 mm; disc achenes 2.4–3 × 1.6–2 mm. Chromosome number: $n = 54$. Figure 21A–D.

Phenology. Flowering period: June to October.

Distribution (Fig. 22). From Yongling Xian, Liaoning in northeast China, west and south through Hebei, Beijing, Shanxi, Shandong, Henan, Shaanxi, Ningxia, and Gansu, including the Loess Plateau and Qinling Mountains in central China, and to Lianyun-gang in northern Jiangsu Province. This taxon grows from low elevations (above 100 m) in the plains regions of east China up to 2200 m at Kangle Xian, Gansu (*W. Y. Hsia 8848*, WUK). At lower elevations it is often found along relatively dry roadsides, whereas at higher elevations it is usually found near irrigation ditches, streams, rivers, or sometimes on open slopes. It was mistakenly recorded from Korea (Nakai, 1911) due to the taxonomic confusion with *K. mongolica*.

In general, populations of *K. lautureana* subsp. *lautureana* in the plains region near the Pacific coast have almost glabrous and entire leaves, whereas those at higher elevations in the Loess Plateau always have leaves loosely covered with short hairs and usually with serrate margins. But exceptions to this pattern are not rare. Some collections from Qingdao and Mt. Tai-shan, Shandong (near the Pacific coast), have crenate and loosely hairy leaves very similar to those of plants from central China

Figure 21. *Kalimeris lautureana*. A–D. *K. lautureana* subsp. *lautureana*. —A. Habit. —B. Phyllary of middle whorl. —C. Leaf. —D. Achene. E–G. *K. lautureana* subsp. *mangtaoensis*. —E. Leaf. —F. Phyllary of middle whorl. —G. Achene.

Figure 22. Geographical distribution of *Kalimeris lautureana* subsp. *lautureana* (dots) and subsp. *mangtaoensis* (circled with C).

(*Y. C. Wang 513* and *639*, PE). There are also continuous intermediates between the two extreme forms. No taxonomic rank is here conferred upon these two forms.

Morphologically, *Kalimeris lautureana* is similar to *K. shimadai*, especially to populations in central China. The main differences are that *K. lautureana* is glabrous or loosely hairy, and has shorter branches and peduncles and broader phyllaries, whereas *K. shimadai* is always densely covered with thin nonglandular hairs interspersed with glandular hairs, and has longer branches and peduncles and narrower phyllaries. These two taxa are sympatric in the southwestern range of *K. lautureana*, namely on the Loess Plateau in central China. Although we have not seen sympatric populations in the field, herbarium specimens of the two taxa are often collected from the same localities, e.g., Lushi Xian, Henan, and Hu Xian, Shaanxi.

The leaves of this subspecies vary from entire to deeply serrate. Yong Ling annotated some specimens with serrate leaves as *Kalimeris lautureana* f. *branchyloba*. Since this kind of variation can been found in almost every species in the genus without any other correlated character states, no taxonomic rank is assigned to these individuals, either.

Additional specimens examined. CHINA. **Liaoning:** Dalian Shi, *Birnie s.n.* (K), *Kitamura s.n.* (KYO), *Stuart s.n.* (BM), *Yabe s.n.* (PE, KYO, TNS); Dandong Shi, Jijiang-shan, Houshan, *W. Wang et al. 1001* (IFP, PE), *Makino s.n.* (MAK); Donggou Xian, Dalu-dao, *S. Y. Li 428* (IFP); Fu Xian, 3 km SE of Delisi, *C. Q. Lin 783* (IFP); Laodong Park, *S. D. Zhao & S. C. Cui 661* (IFP); Jinzhou Xian, Heshang-shan, *Yabe s.n.* (PE); Laohutan, *Kitagawa s.n.* (TI); Lushun Shi, Laotie-shan, *Kitamura s.n.* (KYO, TNS), 200 m, *S. X. Li et al. 6893* (IFP), *C. Wang & Y. X. Liu 982* (IFP, PE), *Sato 24* (TI), *5839* (IFP, PE); Shahekou Station, *Kobayashi 7* (TI); Tieling, *Yamatsuta 111* (TNS); Xifeng Xian, Diaoyutai, Tiehe, *X. C. Jiang et al. 228* (IFP); Longjiren, *Z. F. Fang 109* (IFP), *249* (IFP); Xinbing Xian, Yongling, Xiaochegou, *X. F. Tian 59* (IFP); Xinjin Xian, *Xinjin Bot. Exp. Team 9* (IFP), *56* (IFP). **Hebei:** Beidaihe, *F. Z. Wang 328* (PE); Caojialu, *W. T. Wang 2441* (PE); Jingxing Xian, Jiangyian-shan, *K. M. Liu 3821* (PE, WUK), Fuqingsi, 570 m, *K. M. Liu 3839* (PE, WUK); from Linyuan to Chengde, *Nakai et al. s.n.* (TI); Shanhaiguan, *Yabe s.n.* (PE); Wuling-shan, *W. T. Wang 2441* (PE). **Shanxi:** Datong Xian, Gu-shan, *Hugh 44* (BM); Huo Xian, "Pao-chi," *Hugh s.n.* (BM); Lingbao Xian, Lingbao-shan, *K. C. Kuan & Y. L. Chen 924* (PE); Taibai-shan, 1000 m, *K. S. Hao 4435* (PE), *Hugh s.n.* (BM); "southeastern Shansi," *Licent 11379* (W); "Shensi," *Hugh s.n.* (BM). **Shandong:** Kunyu-shan, forestry station, *Shandong University Team 3103* (PE); Laoshan Xian, Li-cun, 500 m, *Y. C. Wang 639* (PE); Qingdao Shi, Qingdao Bot. Garden, *H. Gu & Y. Gao 289* (MO), *Limmercuamv 241* (G, GH), *277* (G, GH), *283* (LE), *C. Y. Chiao 2978* (GH, IBSC, K, NY, PE); Qixia Xian, Ya-shan, 400 m, *Z. X. Wang 168* (PE); Tai-shan, *Clemens 1512* (E), *Shinagawa 46* (TNS); Wuchimiao, *Y. C. Wang 513* (PE); Yantai Shi, Nanyue, *K. M. Liu 1728* (PE), 100 m, *1828* (PE); Taipingyan, 250 m, *1841* (PE); Qufu-shan, *Faber 163* (GH), *Cowdry 912* (K), *Forbes 1872* (K), *Wawra 1214* (W); Yantai Shi, *Debeaux 80* (P); Zhifu-dao, *Ito s.n.* (TNS), *Williamson s.n.* (E). **Henan:** Lushi Xian, Caomu-chang, 1060 m, *J. Q. Fu 2275* (HIB, KUN, PE, WUK); Shuanghuaishu, 540 m, *919* (HIB, WUK); Mianchi Xian, Shaoshang Forestry Station, 920 m, *Huangtu-gaoyuan Team 1376* (WUK); Mianshan, Qihe River, 1040, *J. Q. Fu 1201* (WUK), *1206* (WUK); Song-shan, 570 m, *K. M. Liu 5532* (PE), *5575* (PE); Xixia Xian, Huilongsi, 1000 m, *Henan Team 1563* (PE). **Shaanxi:** Hu Xian, Laogu, Yinjiapo, 1700 m, *K. T. Fu 14841* (WUK); Huanglong-shan, Shibao, *3131* (PE, WUK); Lantian Xian, Qinggang-xiang, Xiaogou, 1270 m, *G. D. Su 60* (WUK); Long Xian, *P. Ke 234* (WUK); Lueyang Xian, Baishuijiang, Maliutang, 1300 m, *T. P. Wang 18561* (KUN, WUK); Qinling Mts., Baoji, *Fenzel 136* (PE, WUK); Pingli Xian, Shiyan, Nuping, Qinlizi, 1000 m, *Third Yiejin Team 384* (KUN); Taibai Xian, Guaili-xiang, *620 Team 2-357* (PE); Taochuan, Lingdanmiao, 1250 m, *K. T. Fu 9742* (WUK); Taibai-shan, Maomenshang, *S. H. Luo 140* (KUN); Yichuan Xian, Tielumiao, 1050 m, *Huangtu-gaoyuan Team 368* (WUK). **Ningxia:** Jinyuan Xian, 2100 m, *T. P. Wang 13620* (WUK). **Gansu:** Heshui Xian, *Y. H. Sun & Z. S. Jin 252* (WUK); Kangle Xian, Zuguochuan, 2200 m, *W. Y. Hsia 9949* (WUK); Tianshui Xian, Baiyanglin Field Station, 1310 m, *K. M. Liu 10342* (PE, WUK), *10457* (PE, WUK), *10477* (PE, WUK); Dangchuan-qu, Baihua-gongshe, 1550 m, *J. X. Yang 5793* (WUK); Maiji-shan, 1400 m, *K. T. Fu 16260* (WUK); Wudu Xian, 950 m, *T. P. Wang 14891* (PE, WUK); Zhouqu Xian, Jiao'erqiao, 1800 m, *Y. Q. He 686* (PE, WUK); Ziwuling, Lianjiabian, *Z. W. Zhang 2855* (WUK). **Jiangsu:** Lianyungang Shi, Yuntai-shan, *F. X. Liu 10890* (IBSC), *Kanashiro 5615* (KYO).

7b. Kalimeris lautureana subsp. **mangtaoensis** (Kitag.) H. Y. Gu, stat. et comb. nov. *Aster mangtaoensis* Kitag., J. Jap. Bot. 9: 109. 1933. *Kalimeris mangtaoensis* (Kitag.) Kitam., Acta Phytotax. Geobot. 6: 21. 1937. *Aster lautureanus* var. *mangtaoensis* (Kitag.) Kitag., J. Jap. Bot. 13: 554. 1937. *Kalimeris lautureana* var. *mangtaoensis* (Kitag.) Kitag., Lin. fl. manshur. 653. 1939. TYPE: China. Liaoning: Xiaolongshan-dao Island, 10 Sep. 1931, *M. Kitagawa s.n.* (holotype, TI; isotypes, IFP, PE, TI).

Stem about 110 cm tall. Cauline leaves broadly oblong, entire to slightly serrate, 5–7.7 × 1.5–2.4 cm, glabrous. Capitula about 20; peduncles 3.8–6 cm long; bracts 2–4 along the peduncle, the lower ones 7.3–10 × 3–4 mm, the upper ones 4.7–6 × 0.5–1 mm; involucre campanulate, 7–10 mm broad, 6.3–7.8 mm high. Phyllaries in 3–4 whorls, imbricate; those of the outermost whorl 3–4.3 × 1.4–1.9 mm, those of the middle whorl(s) 4.5–6.2 × 2–3 mm, those of the inner whorl 5–7.6 × 2–2.7 mm. Receptacles 2.2–2.5 mm wide, 1.5–1.8 mm high. Ray florets 14–19; ligules 25–28 × 3.5–4.3 mm, the tube 2–2.5 mm long; style 3–4.5 mm long, the branches 1.1–1.5 mm long. Disc florets about 56; corollas 5–5.8 mm long, the lobes unequal, the longer one 1.5–2 mm long, the shorter ones 0.7–1.3 mm long, both 0.5–0.8 mm wide, the tube 1.5–1.8 mm long; anther 1.5–2.1 mm long; style 4–5 mm long, the branches 1.3–1.6 mm long. Ray and disc pappus bristles brownish, unequal; ray bristles 0.3–0.5 mm long; the disc bristles 0.5–0.6(–1) mm long. Achenes were not available from the herbarium specimens. Chromosome number unknown. Figure 21E–G.

Phenology. Flowering period: July to October.

Distribution (Fig. 22). Endemic to Xiaolongshandao (Snake Island) in Bohai, Liaoning Province, China.

This subspecies occurs only on Xiaolongshandao, an island east of the Liaodong Peninsula with an area of about one km². The island was part of the continent and separated from the latter as a result of the break of Liaohe and the deepening of the Bohai Sea under the pressure of the upthrust movement of the Himalaya Mountains (Ji, 1982).

The island is a natural conservation site now because of its endemic Pallas pit vipers, which are reputed to have high medicinal value. The number of vipers on the island is estimated as high as 50,000 (Ji, 1982), which makes the island uninhabitable and traveling very dangerous. The island has been visited only by well-equipped viper catchers and researchers. The available specimens of subspecies *mangtaoensis* were collected by J. Sato in 1933 and 1937.

The main differences between the two subspecies of *Kalimeris lautureana* are that subspecies *mangtaoensis* is less branched, with more and bigger leaves, bigger involucres and phyllaries, and longer pappus bristles than subspecies *lautureana* (Fig. 22). The differentiation between these two taxa may be the result of genetic isolation between them. Although there are only 11 km separating the small island from the closest part of the mainland, gene flow between the two taxa is probably very limited, since *Kalimeris* is dispersed mostly through human activities. The gigantism of this taxon might be caused by high polyploidy.

Additional specimens examined. CHINA. **Liaoning:** Dalian Shi, Xiaolongshan-dao, *Sato 5836* (IFP, PE).

8. Kalimeris integrifolia Turcz. ex DC., Prodr. 5: 259. 1836 ["*Calimeris*"]. *Aster integrifolius* (Turcz. ex DC.) Franch., Mém. Soc. Sci. Nat. Cherbourg 24: 224. 1884. *Asteromoea integrifolia* (Turcz. ex DC.) Loes., Beih. Bot. Centralbl. 37: 189. 1919. *Boltonia integrifolia* (Turcz.) Lauener, Notes Roy. Bot. Gard. Edinburgh 34: 334. 1976. TYPE: Russia. Amur: 1833, *Turczaninow s.n.* (lectotype, here designated, LE; isolectotypes, K, LE).

Asteromoea pekinensis Hance, Ann. Sci. Nat., Bot. sér. 4, 15: 225. 1861. *Boltonia pekinensis* (Hance) Hance, J. Bot. 370. 1867. *Aster pekinensis* (Hance) F. H. Chen, Bull. Fan Mem. Inst. Biol. 5: 41. 1934. TYPE: China. Near Beijing, Oct. 1860, *R. Swinhoe s.n.* (lectotype, here designated, BM; isolectotype, K).

Tap root; perennating by adventitious buds on the upper part of main roots or on the lateral roots. Stem (10–)40–140 cm tall. Cauline leaves narrowly oblong to oblanceolate, entire, (1–)2–5(–6.5) × (0.2–)0.3–0.9 cm, densely covered with appressed uniseriate nonglandular hairs and biseriate glandular hairs on both sides. Capitula usually 25–200 or as few as 5 when growing in harsh habitats; peduncles 2.5–9 cm long; bracts 2–9 along the peduncle, the lower ones 6.1–16 × 1–2.2 mm, the upper ones 2.5–5.2 × 0.4–0.8 mm; involucre hemispherical or rarely campanulate, (3.8–)4.4–8(–9) mm broad, 3–4.6 mm high. Phyllaries in 3–4 whorls, imbricate, densely covered with nonglandular and glandular hairs, sometimes purplish; those of the outermost whorl lanceolate or oblong, 1.8–3.6 × 0.5–1 mm, those of the middle whorl(s) lanceolate to oblanceolate, (2.5–)3–4.2(–5) × 0.8–1.1 mm, those of the inner whorl (3–)3.5–4.5(–5.1)

× (0.6–)0.8–1.1 mm. Receptacles convex to subconical, 1.2–2.3 mm wide, 0.5–1.8 mm high. Ray florets 19–27(–29); corollas pale lilac to light purple, ligules narrowly oblanceolate or oblong to elliptical, (5.2–)6.2–13.5(–15) × (1.1–)1.5–2.5(–2.7) mm, the tube 0.7–1.4 mm long; style 1.5–2.5 mm long, the branches 0.5–1 mm long. Disc florets 42–100; corollas 2.1–3.1(–3.4) mm long, the lobes unequal, the longer one (0.7–)1–1.3(–1.5) mm long, the shorter ones (0.5–)0.7–1 mm long, both 0.4–0.6 mm wide, the tube 0.6–1(–1.2) mm long; anther 0.7–1.2 mm long; style 2–3.3 mm long, the branches 0.6–0.9 mm long, each with a triangular appendage 0.2–0.4 mm long. Ray and disc pappus bristles equal or subequal; ray bristles (0–)0.1–0.3 mm long; disc bristles 0.2–0.4(–0.6) mm long. Achenes greenish or brown, broadly obovate, covered with biseriate glandular hairs at the upper half; margin glabrous or ciliate, 0.1–0.3 mm broad; ray achenes 3(–4)-ribbed, 1.5–2 × 0.9–1.1 mm; disc achenes 2(–3)-ribbed, 1.5–2.2 × 1.1–1.6 mm. Chromosome number: $n = 9, 18$. Figure 23.

Phenology. Flowering period: May to October.

Distribution (Fig. 24). *Kalimeris integrifolia* has a very wide geographical range. It grows in the north along the Amur River, Amur Oblast of Far East region, Russia, extending through eastern and central China to Suzhou, Jiangsu Province, in the southeast and to near Ninglang Yizu Zizhi Xian, Yunnan, in the southwest. It occurs in the following provinces of China: Heilongjiang, Jilin, Liaoning, northern Nei Mongol, Hebei, Beijing, Shandong, Henan, Shaanxi, Jiangsu, Hubei, Sichuan, and Yunnan. It also occurs in Korea from the border with China, through Hambook, Hamnam, Pyongbook, and Pyongnam provinces to Mt. Jangsoo, Hwanghe. It grows from near sea level to 1600 m elevation. This species commonly grows in sunny and dry roadside and river banks, and is most often found at margins of thickets or forests and less often along trails inside forests. Its populations are usually large due to vigorous formation of adventitious buds from the main or lateral roots during the flowering season, except for plants growing on poor soil along dry, open roadsides or river banks.

This species is easily distinguished from the others in the genus by its tap-root system and appressed, nonglandular hairs densely covering both sides of the leaves (Fig. 23). Although it grows sympatrically with *K. incisa* subsp. *incisa*, *K. mongolica*, *K. indica* subspp. *indica* and *stenolepis*, and *K. shimadai* throughout much of its range, no intermediates have been detected so far.

Additional specimens examined. RUSSIA. **Amur:** *Karo 1506* (P), *2767* (GH, MAK). KOREA. **Hambook:** Hoeryong, *Koidzumi s.n.* (KYO). **Hamnam:** Hamhung, *Okuyama s.n.* (TNS). **Pyongbook:** Uiju, *Koizumi s.n.* (KYO). **Pyongnam:** Namp'o (Chinnampo), *Faurie 1073* (BM, E, KYO, W); Pyongyang City, *H. Chung s.n.* (TNS), *Faurie 392* (KYO, P). **Hwanghe:** Mt. Jangsoo, *Koidzumi s.n.* (KYO). CHINA. **Heilongjiang:** Baoqing Xian, Jiefangrun, *Y. L. Zhang et al. 1812* (IFP); Daxing'anling Mts., *Skvortzov s.n.* (GH); Harbin Shi, Guxiang-tun, Laoshantou, *G. Z. Wang & W. Wang 725* (IFP), *G. Z. Wang 834* (IFP); Harbin Agricultural College, 6 (IFP), *C. S. Wang et al. 33* (IFP); Songhuajiang River, *Litvinov 3115* (NY); Taiyangdao to Miaozitaihe, *G. Z. Wang et al. 1015* (IFP), *Dorsett & Dorsett 3698* (NY), *Kitagawa 394* (IFP), *Jettmar s.n.* (W); Jixian Xian, Fuli-tun, *Y. L. Zhang et al. 1833* (IFP); Jiamusi Shi, *P. Y. Fu et al. 56* (IFP); Keshan Xian, Dong-shan, *T. N. Liu et al. 7974* (IFP, PE); Luobei Xian, *C. S. Wang et al. 329* (IFP); Mishan Xian, Peide, *S. X. Li et al. 2913* (IFP); Mishan Xian to Hulin Xian, *Heihuangdi Team 15* (IFP), *R. Y. Li 159* (IFP); Nenjiang River to Heihe River, Jiankeluo, *Y. L. Zhang & T. S. Liu 8* (IFP, KUN); Yichun Xian, Shuangzihe, Xing'an Forestry Station, *N. Liu et al. 7802* (IFP); Yuanhiu Xian, Xigangzi, *G. Z. Wang 177* (IFP). **Jilin:** Changchun Shi, Jinyuetan, *W. Wang et al. 2647* (IFP); Changchun-shi, *Suzuki 13* (KYO), *Nakao s.n.* (KYO), *Komai s.n.* (KYO); Chunhua Xian, Hadamen, *C. S. Wang et al. 2424* (IFP, KUN), *3634* (IFP); Jiutai Xian, Tumenling, Shichangshan, 300 m, *P. Y. Fu et al. 2039* (IFP); Tao'an Xian, *Yamatsuda 98* (TNS); Wuichang to Longhua, Lianhua-shan, *Takahashi s.n.* (TNS); Wangqing Xian, *C. S. Wang 1441* (IFP); Zhenglai Xian, Erjin-cun, *Takano 47* (TNS), *F. H. Chen 579* (GH), *James s.n.* (K). **Liaoning:** Anshan Shi, Anshan Park, *H. Gu & H. Zhang 272* (MO), *273* (MO), *274* (MO); Qian-shan, *278* (MO); Benxi Xian, Pingding-shan, *C. S. Wang et al. 300* (IFP); Dalian Shi, Laohutan, *Kobayashi 20* (KYO); Changhai, Dachangdao, *G. L. Wang 630160* (IFP); Fushun Shi, Dong-gongyuan, *W. Wang et al. 548* (IFP); Fu Xian, Luda, Delisi, *C. Q. Lin 693* (IFP); Fuxin Shi, Shaocaoquian, *M. G. Li 508* (IFP); Huenhe Xian, Huenhe Railway Station, *Sato 9537* (IFP); Jianchang Xian, *C. S. Wang et al. 3155* (IFP); Jinzhou Shi, Huludao, *C. S. Wang 3371* (IFP), *G. Z. Wang 18* (IFP); Xuejia, *Makinon s.n.* (MAK); Liaoyang Xian, Anping-cun, *Sato 10283* (IFP); Bali-cun, *4150* (IFP); Linyuan Xian, Wu'erdeng, Zimeizi, *S. P. Li 167* (IFP); Lushun Shi, Guantou, *Kitamura s.n.* (KYO, MAK), *Suzuki 12068* (TNS); Shengyang Shi, Beilin, *Kato 5184* (TNS); Donglin, *H. Gu et al. 251* (MO), *266* (MO), *268* (MO), *T. N. Liu et al. 343* (IFP, KUN), *Y. L. Zhang 2291* (IFP), *P. Y. Fu 1754* (IFP); Nanhu Lake, *W. Wang et al. 178* (IFP, KUN); Shengyang to Yalujiang River, *Weboter 196* (K); Xifeng Xian, Diaoyu Forestry Station, *S. X. Li & J. L. Zhang 5471* (IFP); Xinshi Xian, Xinshi Railway Station, *Z. F. Fang & Q. S. Wang 2843* (IFP); Yingkou Xian, Shuiyuan, *Yingkou Team 294* (IFP); Zhangwu Xian, Zhanggutai-cun, *T. Wang et al. 2590* (IFP); Zhuanghe Xian, *W. Wang et al s.n.* (IFP). **Nei Mongolia:** E'erguna Qi, 650 m, *D. C. Zhao & T. Wang 1457* (IFP); Kezuofei Qi, Wulanmaodu, Xibei-shan, *P. Y. Fu 2649* (IFP); Hulun Buir Meng, Solon, *Second Humeng Team 336* (IFP), Xiguit Qi, *G. Z. Wang 2820* (IFP). **Hebei:** Baoding Xian, *M. Togashi s.n.* (TNS); Beidaihe, *Cowdry 120* (K), *Licent 7739* (W); Chengde Shi, Ligong, *K. Chujo s.n.* (TNS), *David 2000* (K, P), *2029* (P); Gaoyi Xian, Jing-Han railway, *Kanashiro 3354* (KYO); Xuanhua Xian, Xifang, *Togashi 2641* (KYO). **Beijing:** Prince Park, *T. N. Liu 1122* (E, NY); Xiang-shan, *Sheehan 284-B* (NY), *Bushell s.n.* (K), *Cowdry 106* (K). **Tianjin:** *Bodinier s.n.* (E), *Clemens 2002* (E), *4152* (E), *Licent 1685* (BM), *7761* (BM). **Shandong:** Fei Xian, 300 m, *T. Y. Cheo & L. Yen 230* (BM, E, GH, P, W); Laoshan

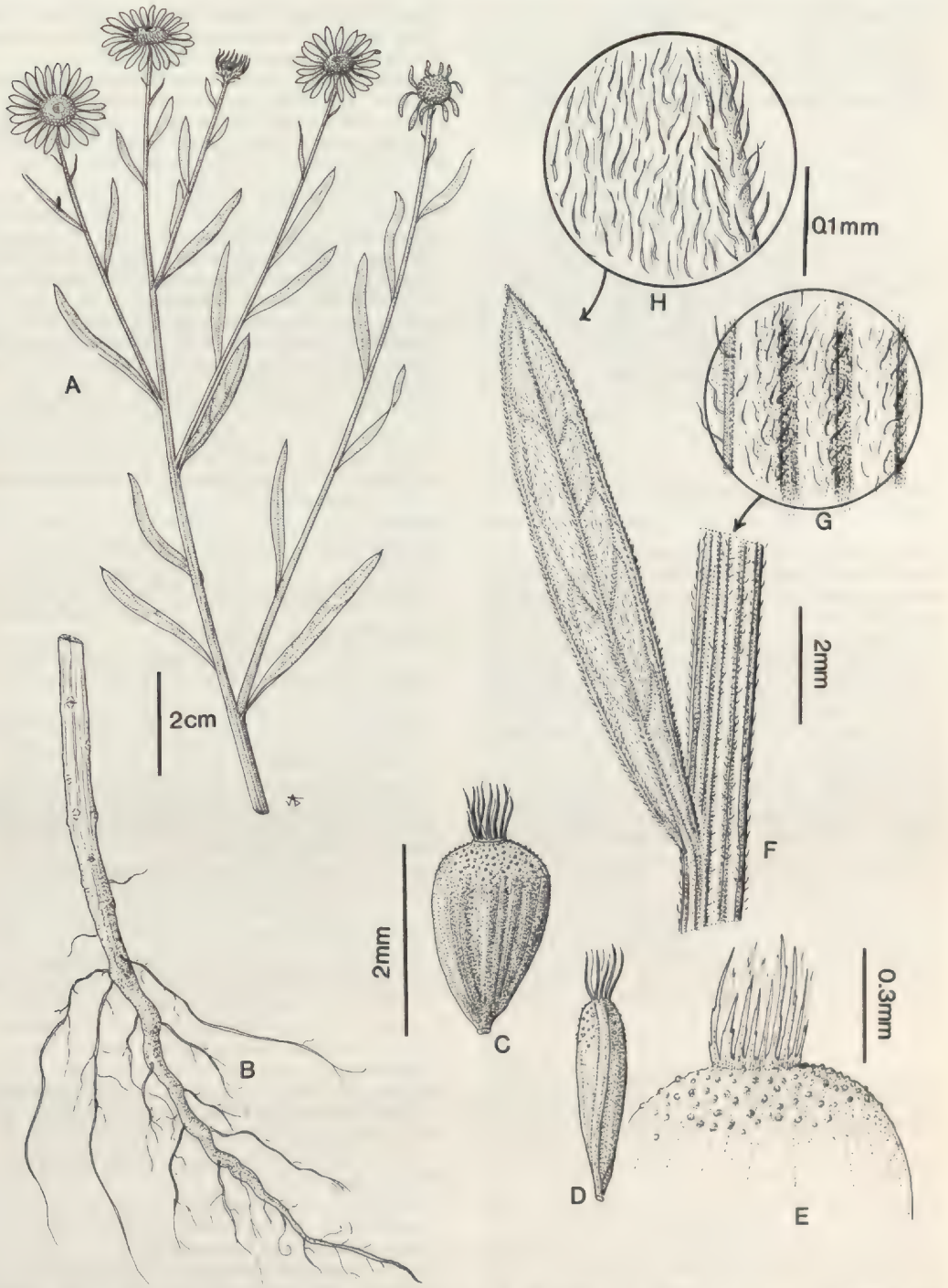

Figure 23. *Kalimeris integrifolia.* —A. Upper branch. —B. Tap root. —C. Front view of achene. —D. Side view of achene. —E. Upper portion of achene. —F. Portion of stem and leaf. —G. Portion of stem showing indumentum. —H. Portion of leaf showing indumentum.

Figure 24. Geographical distribution of *Kalimeris integrifolia.*

Xian, Licun, *H. Gu 301* (MO); Mongying Xian, Hujiagou, *Yamoto s.n.* (BM); Tai-shan, Chaoyangdong, *Shandong University Team 19* (KUN, PE); Weihai Shi, *Elipse 78* (K); Yantai Shi, *Debeaux 63* (P), *79* (P), *92* (P), *Debeaux s.n.* (E), *Forbes s.n.* (E, BM), *Wawra 1269* (W). **Henan:** Lushi Xian, Wulichuan, 480–490 m, *J. Q. Fu 492* (HIB, KUN, PE, WUK). **Shaanxi:** Fuping Xian, Houzhizi-xiang, Damanghe, 1075 m, *X. M. Zhang 332* (KUN, PE); Lueyang Xian, Xiancheng to Wujiaying, 700 m, *K. T. Fu 5964* (KUN, WUK); Zhouzhi Xian, Chenhe-xiang, Qinggangbian, 1560 m, *X. M. Zhang 162* (KUN, PE). **Anhui:** Ma'anshan, *K. Yao 8530* (KYO), *Merrill 1507* (MO). **Jiangsu:** Jinjiang Xian, *Carles 485* (K); Nanjing Shi, Qixia-shan, *C. N. Chen 2058* (W); Xiaolinwei, *Matsuda s.n.* (TI); Zijin-shan, *C. R. Huang s.n.* (TI), *T. N. Liu 493* (NY), *T. K. Nyi 3* (JSBI), *C. N. Chen 8620* (NY, W), *W. C. Cheng 181* (P), *Niederlein 6* (A); Suzhou Shi, *Oka 452* (TI); Xuzhou Shi, *Hori 16* (KYO); Yizheng Xian, Nong-ganxiao, *S. Jiang 8973* (KUN); Zhengjiang Shi, *Migo 34* (KYO), *Oka 22* (TI). **Hubei:** Guanghua Xian, Yuhuashan Forestry Station, *G. H. Chen 193* (HIB); Wuchang Shi, Mo-shan, *H. Gu & D. Chen 132* (MO), *Q. H. Liu 1027* (HIB); Yichang Xian, *Henry 564* (K), *891* (E, K), *2254* (E, K), *4108* (BM, GH, NY); Zhuxi Xian, Majiapuo, *P. Y. Li 7454* (KUN); Epinggongshe, Longwangya, *9490* (KUN). **Sichuan:** Chengdu Shi, Shahebao, *s.c. 2472* (IBCD). **Yunnan:** Ninglang Zizhi Xian, between Yongning and Ninglang, *Forrest 22064* (E, W).

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Numerical List of Species

1a. *K. incisa* subsp. *incisa*
1b. *K. incisa* subsp. *macrodon*
2. *K. pinnatifida*
3. *K. mongolica*
4a. *K. indica* subsp. *indica*
4b. *K. indica* subsp. *collina*
4c. *K. indica* subsp. *stenolepis*
5a. *K. yomena* subsp. *yomena*
5b. *K. yomena* subsp. *angustifolia*
5c. *K. yomena* subsp. *dentata*
6. *K. shimadai*
7a. *K. lautureana* subsp. *lautureana*
7b. *K. lautureana* subsp. *mangtaoensis*
8. *K. integrifolia*

Index to Numbered Collections Cited

The numbers in parentheses refer to the corresponding species in the text and in the Numerical List of Species presented above. Collections marked with asterisk (*) are discussed in more detail in text.

Allison 4 (4c); Amano 6806 (4a); Ando 27 (4a); Anhui Expedition Team 3300 (4a); Anshun Team 665 (4a), 1376 (4a), 1759 (4a), 1903 (4a), 3221 (4b)

Baba 6 (5b), 7 (5b), 11 (5a); Balansa 840 (4a), 4498 (4a); Bao, S. Y. 600 (6), 1500 (6), 1586 (6), 1587 (6); Bao, S. Y. & Yan, S. J. 2209 (4c); Beattie & Kurihara 11119 (2), 11205 (5a); Biji Team 495 (4a), 983 (4a), 1190 (4a), 1564 (4a); Bodinier 1913 (4a), 2474 (4a); Bohnhof 41 (3); Bois 82 (4b); Bois-Reymond 805a (4a); Boufford & Wood 19863 (2)

Cao, Z. Y. 394 (4a), 855 (4a); Carles 438 (6), 485 (8), 799 (4b); Chang, C. C. 4 (6), 5577 (4a), 6510 (4b), 10678 (4a); Chang, H. T. 4690 (4b); Chang, T. C. 2906 (6); Charette 1454 (5a); Chavet 804 (6); Chen, B. Y. et al. 221 (4b); Chen, C. N. 2058 (8), 8603 (4a), 8620 (8), 8621 (6); Chen, F. H. 328 (3); 579 (8); Chen, G. H. 193 (8); Chen, Q. L. 65 (4b); Chen, S. 1829 (4a); Chen, S. Q. 1472 (4b), 11800 (4b), 14007 (4b), 14484 (4b), 16312 (4b), 16760 (4b); Chen, X. B. 173 (4c); Chen, Y. 2137 (4a), 2968 (4a); Cheng, W. C. 181 (8); Cheng, Y. M. 170542 (4a); Cheo, H. C. 65 (4a); Cheo, T. Y. & Yen, L. 230 (8); Chiao, C. Y. 2978 (7a), 14941 (6); Chiao, C. Y. & Fan, C. S. 208 (4a); Chien, S. S. 5320 (4a), 5948 (4a); Ching, R. C. 3629 (4a), 8679 (4c), 10015 (4a), 10260 (4a), 10462 (4a); Chou, H. F. 26593 (4c), 26886 (4c), 26953 (4a), 40593 (3); Chou, K. 2128 (1a); Chou, Y. et al. 2259 (1a); Chow 33 (4a); Chow & Wan 79046 (4b); Chow, H. C. 55 (4c), 207 (4c), 348 (4a), 378 (4c), 4261 (4a), 8940 (4a), 9008 (4a), 18412 (4a); Chow, K. S. 80259 (6); Chuanqian Team 853 (4a), 1823 (4a), 2076 (4a); Chung 473 (1a), 3101 (3), 3107 (1a), 9288 (1a); Chung, H. H. 1702 (4c), 2326 (4b), 2402 (4b), 3815 (4b), 7596 (4c), 9129 (4c); Clemens 1512 (7a), 2002 (8), 4152 (8), 4153 (3); Cowdry 106 (8), 119 (3), 120 (8), 912 (7a); Cui, G. & Lin, C. 1483 (1a), 1499 (1a), 1528 (3), 1668 (3)

Dai, L. Y. & Qian, Z. H. 425 (4c), 922 (4c); Dai, L. Y. et al. 2366 (4c); Dai, T. L. 102239 (4a), 102260 (4a), 102532 (4a), 103190 (4a), 106939 (4a), 107099 (4a);

Dann 54 (1a); David 2000 (8), 2029 (3); Debeaux 63 (8), 79 (8), 80 (7a), 92 (8), 120 (4a); Deng, F. B. et al. 3519 (6), 3726 (6); Deng, L. 2062 (4b), 5081 (4b), 7027 (4b), 7108 (4b), 7972 (4b), 8419 (4b), 8732 (4a), 8736 (4a); Diandongbei Team 507 (4a), 772 (4a), 773 (4a), 892 (4a), 999 (4a); Doi, Y. 40 (5a); Dong, N. C. 1472 (4b); Dorsett & Dorsett 3698 (8); Ducloux 289 (4a), 1585 (4a)

Eberhardt 3284 (4b); Ehara 48 (5a); Elipse 78 (8); Elliott 144 (2)

Faber 163 (7a); Fan, C. S. & Li, Y. Y. 133 (4a); Fan, H. N. 9557 (4b), 9588 (4b), 9610 (4b), 9623 (4b), 9654 (4b), 9718 (4b), 9728 (4b), 9784 (4b); Fang, M. Y. 24783 (4c), 24785 (4c), 24915 (4c); Fang, W. P. 1442 (4a), 12360 (4a); Fang, W. Z. et al. 102 (4a); Fang, Z. F. 109 (7a), 249 (7a); Fang, Z. F. & Wang, Q. S. 2843 (8); Faurie 226 (4a), 392 (8), 393 (1a), 403 (1a), 404 (1a), 1014 (2) 1073 (8), 1141 (4a), 5158 (2), 5159 (2), 6743 (2); Feng, K. M. 10290 (4a); Fenzel 136 (7a), 2471 (4a); Fischer 17 (1a); Forbes 43 (4a), 83 (4a), 927 (4a); Ford 65 (4a); Forrest 3063 (4a), 4005 (4a), 8312 (4a), 11539 (4a), 13025 (4a), 22064 (8) 22424 (4a), 28457 (4a), 30584 (4a); Fortune 124 (4a); Fu, G. X. & Zhang, Z. G. 259 (4c), 260 (4c), 464 (3), 1145 (4a), 1584 (4c); Fu, J. Q. 40 (6), 365 (4a), 492 (8), 565 (4c), 919 (7a), 1201 (7a), 1206 (7a), 2275 (7a); Fu, K. T. 3131 (7a), 3436 (4c), 3590 (6), 4945 (4a), 5513 (4c), 5912 (4c), 5964 (8), 5965 (4c), 6185 (4a), 6326 (4a), 8758 (4c), 9742 (7a), 9764 (4c), 13859 (4c), 14841 (7a), 16260 (7a), 18301 (4c), 18643 (4c); Fu, P. Y. 1754 (8), 2649 (8); Fu, P. Y. & Zhang, Z. H. 451 (3); Fu, P. Y. et al. 56 (8), 959 (3), 2039 (8), 2180 (1a), 4568 (3); Fu, S. X. 110814 (4c); Fudan University Team 50299 (4a), 50531 (6), 52402 (4a); Fujian Botanical Expedition Team 53428 (4b); Fujimura & Fukui 29 (2); Fukuoka c-206 (4c), c-245 (4c), c-258 (4c), 2664 (5b), 7518 (2), 8265 (2), 9887 (5a), 11250 (5b), 11801 (5a), 12298 (5b); Fukuoka et al. 994 (5a); Fung, H. 21109 (4b); Furuse 27 (2), 13944 (2)

Gadlceau 3944 (1a); Gao, Y. Z. et al. 10 (4b); Ging, T. S. 5233 (4b), 5399 (4b), 5667 (4a), 6657 (4a), 7143 (4a); Gu, H. 301 (8); Gu, H. and Chen, D. 121 (4c), 122 (4a), 127 (4a), 132 (8), 134 (4a), 183 (6), 189 (6), 195 (4a), 200 (4a); Gu, H. & Gao, Y. 289 (7a), 292 (4a), 293 (4a), 293a (4a), 295 (4a); Gu, H. & Han, Q. 205 (4c), 206 (4a), 208 (4a), 219 (4c); Gu, H. & Hao, X. 6 (4a), 7 (4a), 8 (4a); Gu, H. & Li, Q. 305 (4a); Gu, H. & Li, Z. 306 (4b), 307 (4b), 308 (4b), 309 (4b), 310 (4b), 314 (4b); Gu, H. & Jiang, M. 304 (4a); Gu, H. & Noguchi 418 (5a), 420 (5b), 421 (5a), 422 (5a), 423 (5a), 424 (5a), 425 (5a); Gu, H. & Takahashi 386 (5a), 389 (5b), 392 (5b), 393 (5b), 395 (5b), 397 (5b), 398 (5a), 400 (5a), 401 (5b), 402 (5a), 403 (5a), 404 (5a), 405 (5b), 406 (5a), 407 (5b), 408 (5b), 410 (5a), 411 (5b); Gu, H. & Yahara 315 (2), 322 (2), 323 (2), 325 (2), 326 (2), 326a (2), 327 (2), 328 (2), 330 (2), 426 (2), 427 (2), 428 (2), 429 (2), 430 (2); Gu, H. & Zhang, H. 272 (8), 273 (8), 274 (8), 278 (8), 283 (3), 284 (3), 286 (3), 288 (3); Gu, H. & Zhang, W. 276 (1a), 279 (1a), 280 (1a); Gu, H. et al. 249 (3), 251 (8), 257 (3), 263 (3), 264 (3), 265 (3), 266 (8), 266a (1a), 267 (3), 268 (8), 269 (3), 270 (1a), 348 (5b), 349 (5a), 350 (5a), 351 (5a), 352 (5a), 353 (5b), 354b (5b), 354c (5b), 354d (5b), 355 (5b), 356 (5b), 357a (5a), 359a (5b), 360 (5b), 363 (5b), 365 (5b), 367 (5b), 368 (5a), 369 (5b), 370 (5a), 370a (5b), 371 (5a), 371a (5a), 372 (5b), 373 (5a), 374 (5a), 375 (5b), 377 (5a), 379 (5b), 381 (5a), 382 (5a), 383 (5a), 384 (5a), 385 (5a), 412 (5a), 414 (2), 415 (2); Guan, K. J. 1963 (4a), 74457 (4a); Guan, K. J. & Wang, W. T. 1594 (4a), 2264 (4a), 2629 (4a); Guan, K. J. et al. 725 (4a), 854 (4a); Guangxi Team 3760 (4a); Guangzhou Qisi Team 4956 (4b); Guizhou Team 3581 (4b), 3947 (4b), 4107 (4a), 7063 (4a), 7412 (4b), 8053 (4b); Guo, B. Z. 48 (4c), 1839 (4c), 3996 (6); Guo, Q. F. 140036 (4b)

Handel-Mazzetti 2694 (4b); Hao, K. S. 4435 (7a), 37699 (4a); Hashimoto 754 (5a, 5c)*, 4670 (2), 4714 (5b), 13500 (5b); Hatusima 17309 (4a); Hatusima & Sako 27950 (5a), 30887 (4a); Hautefenille 161 (4a); He, S. B. 547 (4c), 735 (4c); He, X. Y. 24938 (4a), 25882 (4a), 26204 (4a), 27448 (4a), 29842 (4a); He, Y. Q. 686 (7a), 1102 (4a), 14897 (4a); Heihuangdi Team 15 (8); Heilongjiang Expedition Team 142 (1a), 151 (1a), 205 (1a); Hemmi 355 (2); Henan Team 1563 (7a), 2080 (4a); Henry 70 (4c), 89 (4a), 216 (4a), 384 (4a), 564 (8), 835 (4c), 891 (8), 1051 (4c), 1343 (4c), 2099 (4c), 2254 (8), 2474 (4c), 2739 (6), 2739a (4c), 4108 (8), 5209 (4a), 7204 (4c), 9754 (4a); Hino et al. 62 (2); Hiroe 5071 (5b), 5113 (5a), 5120 (5a), 6441 (5a), 16362 (2); Honda 190 (4a), 638 (4a); Hong, T. & Keng, P. K. 348 (4c); Hori 16 (8); Hotta 10181 (2); Howell 95 (4a); Hsia, W. Y. 1945 (3), 4744 (6), 4748 (6), 6338 (4a), 9949 (7a); Hsiung, T. N. 539 (4a), 559 (4a), 616 (4a); Hu, Q. M. 2966 (4a), 3375 (4b), 4223 (4a), 5297 (4a), 5522 (4a), 44617 (4b); Hu, Q. Z. 3 (4a); Hu, W. G. & He, Z. 12026 (4a); Hu, Y. Y. & Wen, S. K. 580599 (4a), 580715 (4a); Huadong Field Station Team 2974 (6), 3170 (4a), 3773 (4c), 3776 (6), 4274 (4c), 4488 (6), 4795 (4a), 5475 (6); Huang, C. 165222 (4a); Huang, R. H. 56 (4c), 1070 (4c); Huang, Z. 37257 (4b), 42103 (4b), 42350 (4b), 43384 (4b); Huanghe and Ganyi Teams 1835 (4c), 1939 (4c); Huangtu-gaoyuan Team 368 (7a), 487 (4c), 1276 (4c), 1376 (7a), 1969 (6); Hubei Expedition Team 24197 (4a); Hugh 44 (7a)

Inoue & Im 2252 (5a); Ito, H. 9 (2); Ito, T. 510 (4a); Iwasaki 2 (4a); Iwatsuki 3486 (5a); Iwatsuki & Koyama 37 (2); Iwatsuki et al. T 9428 (4a)

Jiang, S. 8973 (8); Jiang, X. C. et al. 228 (7a); Jiang, X. M. 35676 (4a); Jiangxi Team 835 (4a), 2419 (4a); Jiangxi Teachers' College Team 12037 (4b); Jilin Teachers' College Team 788 (3)

Kanai 419 (2), 6481 (2), 731271 (2); Kanasiro 18 (4a), 3354 (8), 4130 (3), 4757 (4a), 4838 (6), 5615 (7a); Kanblack 273 (4a); Karo 182 (1a), 1506 (8), 1507 (1a), 2767 (8); Kato 5184 (8); Ke, P. 234 (7a); Keng & Kao 1276 (4a); Kirino 386 (2); Kitagawa 394 (8), 1535 (2), 5361 (2); Kitamura & Murata 2079 (2); Kobayashi, K. 20 (8); Kobayashi, M. 7 (7a); Kobayashi, S. 3485 (2), 4294 (2), 13126 (2); Koidzumi, H. 27236 (5a), 65094 (5a); Koidzumi, G. 94955 (2); Kokano 8 (5b), 19 (5b); Kolshaff 95 (6); Komarov 1507 (1a), 1507b (3), 1510 (3); Konta 11564 (2); Koyama 220 (2), 407 (2), 775 (2), 1492 (2), 2979 (5b), 7311 (2), 7541 (5a), 7550 (5b); Kozlow 14382 (3), 14389 (3); Kuan, K. C. & Chen, Y. L. 924 (7a); Kung, H. W. 2845 (4c), 3737 (6); Kurachi 7926 (2); Kurihara 99 (5a); Kurihara et al. 160 (2); Kuriyama 2009 (5b); Kurosaki 2116 (2), 2298 (2), 2607 (5a), 6542 (5b), 8019 (2), 9537 (5b), 9716 (5a), 11017 (5a), 11104 (2), 11365 (2), 11432 (2), 11585 (5a), 11893 (2), 12069 (2), 12928 (5b), 13656 (5a), 13994 (5a), 140001 (5b), 14560 (5a); Kurosaki & Kato 22 (5b), 148 (5a); Kurosaki et al. 2705 (5b)

Lace 5841 (4a); Lai, S. S. 1651 (4a), 1797 (4b), 3134 (4c); Lai, S. S. & Nie, M. X. 3809 (4a); Lai, S. S. et al. 5290 (4b); Lan, S. K. 664 (4b), 2152 (4b); Lau, S. K. 4097 (4b), 4757 (4b), 28542 (4b); Lau, S. Y. 20551 (4a); Law, Y. W. 1220 (4c); Lecomte & Finet 93 (4b); Lee, T. B. et al. 6627 (1a), 6826 (1a); Legendre 94 (4a); Levine 272 (4a), 1081 (4a), 3446 (4b); Li, C. L. 1938 (4a); Li, G. L. 63217 (4a), 63279 (4a); Li, H. J. 4767 (4c), 4791

(4c), 5307 (4c), 5486 (4c); 5757 (4c), 6246 (4c), 6493 (4c), 6530 (4c), 6623 (4c), 7229 (4c), 8739 (4c), 8900 (4a), 9051 (4a), 9387 (4c); Li, M. G. 508 (8); Li, P. Y. 14 (4a), 42 (4c), 94 (4a), 378 (4c), 785 (4a), 988 (4c), 1710 (4c), 3308 (4a), 4223 (4a), 4420 (4a), 4843 (4c), 5501 (4a), 5560 (4a), 5620 (4a), 5963 (4a), 6799 (4a), 6813 (4a), 6909 (4a), 7004 (4a), 7056 (4a), 7211 (4a), 7330 (4a), 7454 (8), 7574 (4a), 7928 (4a), 8153 (4a), 8439 (4c), 8512 (4a), 8631 (4a), 8723 (4a), 8797 (4a), 9101 (4a), 9178 (4a), 9427 (4a), 9490 (8), 9635 (4a), 9976 (4a), 11118 (4a), 109010 (4a); Li, R. Y. 159 (8); Li, S. 760 (1a); Li, S. et al. 4655 (1a); Li, S. P. 167 (8); Li, S. X. & J. L. Zhang 5471 (8); Li, S. X. et al. 2913 (8), 6893 (7a); Li, S. Y. 428 (7a); Li, X. G. 202385 (4b), 202806 (4b); Li, Y. et al. 821 (1a); Li, Y. K. 401235 (4b); Liang, B. H. 12882 (4a); Liang, C. F. 30624 (4b); Licent 9 (3), 1579 (3), 1685 (8), 2422 (6), 7739 (8), 7761 (8), 11379 (7a), 12506 (6), 12526 (4c); Limmercuamv 241 (7a), 277 (7a), 283 (7a); Lin, C. Q. 693 (8), 783 (7a); Ling, K. 2310 (6); Ling, Y. 2174 (4b), 2965 (4b), 3248 (4b), 3281 (4b); Lipuo Team 2249 (4b); Litvinov 2556 (1a), 3115 (8); Liu, C. S. 1584 (6); Liu, F. X. 10890 (7a); Liu, J. M. 10477 (4a); Liu, K. M. 1728 (7a), 1828 (7a), 1841 (7a), 3821 (7a), 3839 (7a), 4842 (4a), 5532 (7a), 5575 (7a), 8574 (4c), 8692 (4c), 8995 (4c), 9039 (4c), 9048 (4c), 10342 (7a), 10457 (7a), 10477 (7a); Liu, K. R. 393 (4c), 774 (4c); Liu, L. H. 9357 (6); Liu, L. H. & He, G. Z. 16483 (4a); Liu, N. et al. 7802 (8); Liu, Q. F. 30164 (4b); Liu, Q. H. 1027 (8), 1073 (6); Liu, S. 3685 (1a); Liu, S. et al. 1282 (1a), 1363 (1a), 1802 (1a), 8298 (1a); Liu, S. L. et al. 18 (4a); Liu, T. N. 493 (8), 1122 (8), 9854 (6); Liu, T. N. & Tsoong, P. C. 75 (6), 2170 (4a), 2365 (4a), 3500 (4a), 3668 (4c); Liu, T. N. & Wang, C. 50 (4a), 107 (4c), 342 (4c), 919 (3); Liu, T. N. et al. 338 (3), 343 (8), 7974 (8), 10275 (3); Liu, T. W. 697 (6), 749 (6), 751 (6); Liu, X. Q. 25137 (4b), 28542 (4b); Liu, Y. G. 2538 (4b); Liu, Z. F. & Zhou, T. P. 1439 (4a), 1781 (4c), 1983 (4a), 2697 (4a); Long, X. Z. 241 (4c); Long, Y. Z. 254 (4c); Luo, S. H. 140 (7a)

Maclagan 124 (4b); Maekawa. 7 B54 (4a), 8 B22 (4a), 9 B34 (4a), 160 A32 (2), 741 (4a), 745 (4a), 119228 (4c); Maire 50 (4a), 351 (4a), 454 (4a), 525 (4a), 2561 (4a), 2568 (4a); Makino 2 (2), 28 (2), 44 (5a), 149 (2), 169 (4a); Masamune 14176 (2); Maruyama 512 (5b), 924 (5b), 925 (5b); Mayebara 5800 (5a); Mengning Team 1150 (3); Merrill 1507 (8), 1509 (4a), 1526 (6), 10021 (4a); Michaelis 78 (4c); Midorikawa 508 (2), 540a (2), 540b (2), 661 (2), 1028 (2), 1368 (2), 1729 (2), 2002 (2); Migo 34 (8), 35 (4a), 36 (4a), 37 (4a), 38 (4a), 41 (4a), 42 (6), 43 (4a), 44 (4a), 45 (6), 61 (6), 64 (4c), 65 (4a), 66 (4a); Mills 136 (1a), 141 (3), 145 (1a), 410 (1a); Mimoro et al. 1162 (2), 4008 (5a); Miyagi 7277 (4a); Miyamoto 80 (5b), 105 (5b); Mizushima 12032 (2); Momiyama 18 (2); Momora 1862 (5b); Mori 53 (2), 195 (3), 282 (3), 335 (4a); Mu, D. Y. 297 (6); Murai 33 (5b); Murata, G. 6716 (2), 8355 (5a), 11818 (2), 12631 (5a), 12681 (5a), 13430 (2), 13232 (2), 14327 (5a), 14351 (2), 17491 (2), 18437 (5a), 19036 (5c), 19038 (5b), 19662 (5a), 20083 (5a), 27445 (2), 27540 (2), 44563 (2), 46619 (5b); Murata, G. & Koyama 41306 (2), 44480 (5a); Murata, G. & Nishimura 270 (5b), 293 (5c); Murata, G. & Shimizu 329 (2), 1472 (2); Murata, G. & Tabata 49 (2); Murata, G. & Togashi 4 (5a), 11 (5c), 25 (5c), 36 (5c), 38 (5c), 39 (2); Murata, G. et al. 126 (5a), 128 (5b), 33895 (2); Murata, J. 6075 (2), 6682 (5b), 6692 (5b), 6864 (5b), 8415 (5a), 9908 (2), 10069 (5a), 11496 (4a), 114890 (5a); Murata, J. & Ohba 5382 (2); Murata, J. et al. 4496 (5a), 6257 (2), 15419 (5b), 33871 (5c); Murata, K. 1610 (2)

Nagasawa 66 (4a), 523 (4a); Nagata 2457 (4a); Nakai 2534 (5a), 2773 (1a), 2785 (1a), 3592 (1a), 6519 (1b), 6520 (4a), 6522 (1b), 13218 (1a); Nakajima 86 (5b), 10998 (5b), 15499 (5b), Nakashima 16552 (5a); Nanba 8160 (5b); Nanjing Forestry College Team 7800-447 (4a), 7800-746 (6); Naruhashi 1856 (2); Nie, M. X. 4681 (4a), 5172 (4a); Nie, M. X. & Chen, S. L. 7418 (4a); Nie, M. X. & Lai, S. S. 3508 (4a), 4152 (4a), 4681 (4a), 5172 (4a); Nie, M. X. et al. 3031 (4a), 9650 (4b), 9757 (4b); Niederlein 6 (8); Ningxia Team 1-0228 (4a); Nitta & Mabuchi 12012 (2); Nomura, N. 53 (1a); Nomura, Y. 3 (5a); Nyi, T. K. 3 (8)

Ogura 2458 (2); Ohashi, H. et al. 1546a (2); Ohba 48 (4a), 61101 (5a), 652000 (5a), 718022 (2); Ohba & Akiyama 1987 (2), 2559 (5a); Ohwi 1002 (5a); Oka, K. 3647 (5a), 3671 (5b), 6496 (5a), 6497 (5a), 22925 (5b), 34250 (5a), 37697 (5a); Oka, S. 22 (8), 452 (8); Okamoto, K. 690 (5a, 5c)*; Okamoto, S. 16067 (1a), 16068 (1a), 19677 (5b), 19678 (5a); Okuyama 17476 (5a), 17580 (5c), 18011 (5a), 23799 (5c); Okuyama & Utsumi 11470 (5a); Oldham 244 (4a), 399 (5b); Ou, L. S. 150 (4b); Oouchi & Okuyama 20385 (5a)

Pai, Y. Y. 1168 (4c), 1282 (6), 1340 (4a), 1399 (6); PE Team 1585 (3); Pei, C. 8083 (4a); Peng 46699 (4a); Peng, D. Y. 45389 (4a); Petelot 400 (4a); Ping, T. K. 1884 (4b); Pu, P. Y. & Chou, Y. L. 2180 (3)

Qian, J. 850 (1a), 955 (1a); Qianbei Team 1781 (4a), 2329 (4b), 2336 (4a), 2697 (4a), 3065 (4a), 3723 (4a); Qiannan Team 2329 (4a); Qiao, Y. L. 108 (4a), 353 (4a); Qiu, B. Y. 50787 (4a), 60231 (4a), 77126 (4a), 77566 (4a), 77613 (4a)

Radde 86 (1a); Rechinger 2260 (4b); Rock 41 (3)

Saberkin 613 (1a), 770 (1a); Saimi 5857 (5a); Saito 270 (5b), 1568 (1a); Sakata 498 (1a); Sato 24 (7a), 1188 (3), 4150 (8), 5836 (7b), 5839 (7a), 5842 (3), 5849 (3), 8870 (3), 9537 (8), 10219 (3), 10220 (3), 10283 (8), 10287 (3); Schindler 308a (4a); Schnack 135d (3); Second Humeng Team 336 (8); Shandong University Team 19 (8), 3103 (7a); Sheehan 284-B (8); Shengnongjia Team 21777 (4c); Shi, G. L. 12093 (4b), 13241 (4b); Shigeru 200 (5a); Shimada 5471b (4a), 5472b (4c), 12991 (5a), 12993 (5b), 13019 (5a); Shimizu et al. T11662 (4a); Shinagawa 46 (7a); Shinota 5386 (2); Shiota 689 (2), 8134 (5a); Shixing Team 172 (4b); 1980 Sino-Amer. Bot. Expedition 1105 (4c); 620 Team 2-357 (7a), 3-357 (6); Smith, H. 6180 (4c), 6429 (4c), 7677 (6); Steward & Cheo, C. C. 1077 (4b); Steward et al. 51 (4a), 450 (4a); Su, G. D. 60 (7a); Sun, S. C. 772 (4a), 830 (4c), 849 (4a), 1239 (4a), 1259 (4a); Sun, S. C. & Chang, K. 667 (4a), 1170 (4a), 1206 (4a), 1417 (4a), 1772 (4a); Sun, S. L. 982 (4a); Sun, Y. H. & Jin, Z. S. 252 (6); Suzuki, M.13 (8); Suzuki, T. 12068 (8)

Tagawa 106 (2), 2989 (2), 6748 (5a); Tagawa & Iwatsuki 1991 (2), 2442 (4a); Takahashi, H. 2838 (2); Takahashi, K. 215 (5c); Takahashi, M. 547 (3), 860 (3), 1702 (5a); Takahashi, N 102 (2); Takaki 327 (5b); Takano 47 (8); Takato 311 (5a); Takenaka 198 (2), 203 (2); Tamura & Koyama 32106 (6); Tan, P. X. 58868 (4b), 59479 (4b), 59944 (4b), 60363 (4b), 60368 (4b), 60369 (4b); Tanaka 93 (4a), 13885 (5a); Tang, C. C. & Ma, S. E. 2906 (4b); Tang, C. L. 399 (4c), 561 (4c), 976 (4a); Tang, S. G. 5706 (6); Tang, T. & Hsia, W. Y. 196 (4a); Taquet 226 (4a), 950 (1b), 951 (1b), 952 (1b), 990 (1b), 991 (1b), 992 (1b) 6236 (1b), 9679 (4a); Tateishi et al. 4363 (2), 4496 (5a), 4563 (2); Tatewaki 31540 (3); Tawada 3 (4a); Teng, S. W. 233 (4c), 90735 (4b); Terabayashi 728 (5b); Third Yiejin Team 384 (7a); Tian, X. F. 59 (7a); Togashi 2641 (8); Tomioku 5972 (2); Torii 2388 (2), 2392 (5a); Toyama & Okuyama

18770a (5b); Tsai, H. T. 53509 (4a), 53573 (4a), 60729 (4a), 61066 (4a), 62482 (4a), 62827 (4a); Tsang, W. T. 776 (4b), 20844 (4a), 21400 (4b), 21594 (4b), 22759 (4b), 22994 (4b), 23247 (4b), 28036 (4b); Togashi 2641 (8); Tsiang, Y. 1189 (4b), 3282 (4b), 10223 (4a), 10770 (4a); Tsiang, Y. & Wang, H. 16414 (4a); Tsoong, P. C. 26 (4b), 39422 (4a); Tsuchiya, K. 2121 (5a); Tsui, T. M. 696 (4b); Tsutsui, S. 25505 (5a), 27260 (5a), 27532 (5a); Tung, Y. Y. 123 (4a)

Umemura 6 (5b); Uno 94 (5b), 22976a (1a)

Wang, C. 40255 (4b); Wang, C. & Liu, Y. X. 982 (7a); Wang, C. S. 128 (1a), 1441 (8), 172 (1a), 508 (3), 3371 (8); Wang, C. S. et al. 33 (8), 72 (3), 300 (8), 329 (8), 1846 (3), 1897 (3), 2138 (3), 2367 (3), 2371 (3), 2373 (3), 2381 (3), 2386 (3), 2390 (3), 2424 (8), 2644 (3), 3155 (8), 3180 (3), 3451 (3), 3452 (3), 3453 (3), 3524 (3), 3634 (8), 3772 (3), 3820 (3), 3830 (3), 3855 (3), 3868 (3), 4231 (3); Wang, C. W. 80971 (4a); Wang, F. T. 453 (4a), 2247 (4a); Wang, F. Z. 328 (7a); Wang, G. 498 (1a); Wang, G. & Li, Q. 26 (1a); Wang, G. L. 630160 (8); Wang, G. Z. 6 (8), 18 (8), 177 (8), 321 (3), 834 (8), 2820 (8); Wang, G. Z. & Wang, W. 725 (8); Wang, G. Z. et al. 1015 (8), 1018 (3); Wang, H. 41433 (4a); Wang, H. C. 912 (4a), 4093 (4a); Wang, J. W. & Wu, F. T. 120 (4c); Wang, Q. S. 78 (4a), 302 (4c), 306 (4c), 370 (4c); Wang, T. 1671 (1a), 2465 (1a), 2572a (1a); Wang, T. et al. 2182 (1a), 2590 (8), 2721 (3); Wang, T. P. 887 (4a), 1436 (6), 2957 (6), 3626 (6), 5045 (6), 5062 (6), 5975 (6), 8282 (4a), 8910 (4a), 10791 (4c), 11322 (4c), 11865 (4a), 12098 (4a), 13620 (7a), 14891 (7a), 15931 (4c), 16022 (4a), 16313 (6), 17106 (4a), 18561 (7a); Wang, W. T. 2441 (7a), 67644 (4a), 67686 (4a); Wang, T. W. & Liu, Y. 82264 (4a), 84131 (4a); Wang, W. 3526 (3); Wang, W. et al. 178 (8), 454a (3), 548 (8), 1001 (7a), 2647 (8), 2656 (3); Wang, X. W. et al. 192 (4b); Wang, Y. C. 513 (7a), 639 (7a); Wang, Z. X. 168 (7a); Wawra 1214 (7a), 1269 (8); Weboter 196 (8); Wei, Z. P. 1047 (4c), 1966 (4c), 2044 (4c), 3855 (4a), 12199 (4b); Wenyon 1887 (4a); Wilson 1693 (4c), 1703 (4a), 1727 (6); Wright 142 (4a); Wu, K. M. 60165 (4b), 60435 (4b)

Xiamen University Team 333 (4b); Xing, J. Q. 1075 (4c), 7992 (4a), 9342 (4a), 9660 (4c), 10063 (4a), 10308 (4a), 10555 (4c), 10652 (4c), 10901 (4c), 10975 (4c), 11073 (4c), 11273 (4c), 11679 (4c), 12096 (4c), 12619 (4c), 12738 (4c), 12820 (4c), 13056 (4c), 13089 (4c), 17789 (4c), 17990 (4c); Xinjin Bot. Exp. Team 9 (7a), 56 (7a); Xiong, J. H. & Chou, Z. Y. 91840 (4a), 92444 (4a), 94009 (4a); Xiong, S. 7109 (4a); Xiong, Y. G. 10070 (6); Xu, X. H. & Lin, H. F. 153866 (4b); Xu, Y. B. 10051 (4b)

Yamamoto 384 (5a), 386 (5a), 3446 (5a); Yamanaka 26157 (5a), 54349 (5a); Yamasaki 8986 (2); Yamatsuta 13 (2), 80 (3), 84 (3), 85 (3), 87 (1a), 93 (1a), 94 (3), 98 (8), 99 (1a), 104 (3), 105 (3), 111 (7a), 114 (3), 115 (3), 277 (3), 290 (3), 4050 (2), 4299 (5a); Yamazaki et al. 425 (5a); Yang, G. H. 56939 (4a), 65084 (4a); Yang, J. X. 1441 (4a), 2085 (4c), 5793 (7a); Yang, X. J. 3625 (6); Yang, X. X. 10836 (4a); Yang, Z. B. & Yao, J. 1164 (4c); Yao, K. 8530 (8); Yao, Z. W. 4042 (4a); Ye, H. H. 462 (4b); Yi, W. Q. 60-1238 (4a); Yingkou Team 294 (8); Yogo 3557 (5a); Yoshioka 12 (5a); Yoshinaga 523 (4a); Yu, P. H. 489 (4a), 992 (4a); Yue, J. S. et al. 1706 (4b), 2181 (4a), 2826 (4b), 3865 (4a), 3865 (4b), 4894 (4a)

Zhan, X. X. et al. 1067 (4a); Zhang et al. 1864 (3); Zhang, G. C. et al. 81 (4b); Zhang, H. D. 1929 (4b); Zhang, R. M. 679 (4c); Zhang, R. Z. 25652 (4c), Zhang, S. Y. 1052 (4a), 4194 (4a), 6828 (4a), 7107 (4a); Zhang, X. M. 162 (8), 332 (6), 332 (8); Zhang, X. Y. 1131 (4a); Zhang, Y. & Wang, S. 657 (1a); Zhang, Y. et al. 1226 (1a), 2117 (1a); Zhang, Y. L. & Liu, T. S. 8 (8); Zhang, Y. L. et al. 945 (3), 1812 (8), 1833 (8), 2291 (8), 2292 (3); Zhang, Z. R. 25884 (4c); Zhang, Z. W. 2855 (7a); Zhang, Z. Y. 189 (4a), 662 (6), 1237 (4c), 3541 (4c), 3617 (4c), 3789 (4c), 6366 (4c), 6573 (4c), 6839 (4c), 7065 (4c), 7094 (4c), 7884 (4c), 8827 (4c), 9240 (4c), 10815 (4c), 11802 (4c), 13029 (4c), 13732 (4c), 14791 (4a), 16908 (4a); Zhao, D. C. & Wang, T. 1457 (8); Zhao, S. D. & Cui, S. C. 661 (7a); Zhao, Q. S. & Liu, S. S. 5704 (4a); Zhao, Z. X. 550 (4a), 890 (6); Zhejiang Team 27655 (4a); Zhejiang Expedition Team 28893 (4c), 29121 (4c), 29159 (4c); Zheng, J. H. 96 (4c); Zheng, Z. 101 (4c); Zhong, S. Q. A60092 (4b), A60821 (4b), A60881 (4b), A62622 (4b); Zhou, H. B. 3021 (6); Zhou, T. P. & Liu, Z. F. 2421 (4b); Zollinger 895 (4a), 899 (4a)

A REVIEW OF THE GENUS *CYDISTA* (BIGNONIACEAE)[1,2]

Warren D. Hauk[3]

ABSTRACT

Cydista (Bignoniaceae) is a genus of six primarily lowland species ranging from central and southern Mexico to Paraguay and eastern Brazil. All species are lianas with showy white to magenta campanulate-funnelform flowers, linear to linear-oblong fruit, and winged seeds. This paper builds on the work of the late Alwyn H. Gentry and utilizes an extensive database produced from his investigations. Descriptions, separate keys to flowering and fruiting material, maps of species distributions, graphs of flowering and fruiting phenology, and an illustration are presented.

The genus *Cydista* (Bignoniaceae) belongs to tribe Bignonieae, which is composed almost exclusively of lianas. All six *Cydista* species are lianas that produce showy white to magenta, campanulate-funnelform flowers, frequently with conspicuous nectar guides (Fig. 1). As one of several closely related genera, *Cydista* differs from its allies in its cymose inflorescences, 2-foliolate leaves, simple tendrils, linear-lepidote ovary, and medium reticulate pollen (Gentry, 1978; Gentry, Flora de Colombia ms., unpublished; Gentry & Tomb, 1979). Other characters that are useful to distinguish *Cydista* are stems with eight phloem arms in cross section and the absence of both a nectariferous disk and interpetiolar glandular fields. *Cydista* has no established infrageneric classification. One species, *C. aequinoctialis* (L.) Miers, has two recognized varieties.

The late Alwyn H. Gentry treated *Cydista* in several regional floras, but his monographic work did not encompass *Cydista* or any other genera of the liana tribe Bignonieae. This paper utilizes the vast amount of information chronicled by Gentry in his studies of Bignoniaceae, compiles these sources of information on *Cydista* into a single treatment, and maintains the fundamental species concepts employed by Gentry, because there is ample evidence to support his taxonomic hypotheses. The database established by Gentry's investigations has allowed production of detailed maps of geographic distribution (Figs. 2–6) and graphs of flowering and fruiting phenology (Figs. 7–14). The new distribution and phenology data presented here provide an important foundation for future investigations of taxonomy and speciation in *Cydista*.

HISTORY

John Miers first described *Cydista* in 1863, based on *Bignonia aequinoctialis* L., and transferred *Bignonia diversifolia* Kunth to *Cydista*. At least five other species names were published that are now regarded as synonymous with *C. aequinoctialis* [*C. amoena* Miers, *C. incarnata* Miers, *C. seemannii* Miers, *C. spectabilis* (Vahl) Miers, and *C. pubescens* S. F. Blake], and one that is synonymous with *C. diversifolia* (Kunth) Miers [*C. vargasiana* (DC.) Miers]. In 1919, Loesener transferred *Arrabidaea potosina* into *Cydista*, and in 1940 Seibert described *C. heterophylla* from material collected in the Yucatán Peninsula of Mexico. Until the work of A. H. Gentry, no other lasting additions to *Cydista* were made. Gentry (1977b) transferred *Anemopaegma decorum* S. Moore into *Cydista*, and the following year described material from Venezuela as a new species, *C. lilacina* A. H. Gentry. Historically, species of *Cydista* have been placed in numerous other genera (i.e., *Bignonia, Arrabidaea, Temnocydia, Levya, Anemopaegma, Clytostomanthus,* and *Pleonotoma*), a fact that illustrates the difficulty surrounding delimitation of generic boundaries in Bignoniaceae. At least two other currently recognized species of Bignoniaceae, *Mansoa difficilis* (Cham.) Bureau & K. Schum. and *Roentgenia bracteomana* (K. Schum. ex Sprague) Urb., were originally described as species of *Cydista*.

SYSTEMATICS

As traditionally circumscribed, *Cydista* is one of a group of closely related genera that possess an

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[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

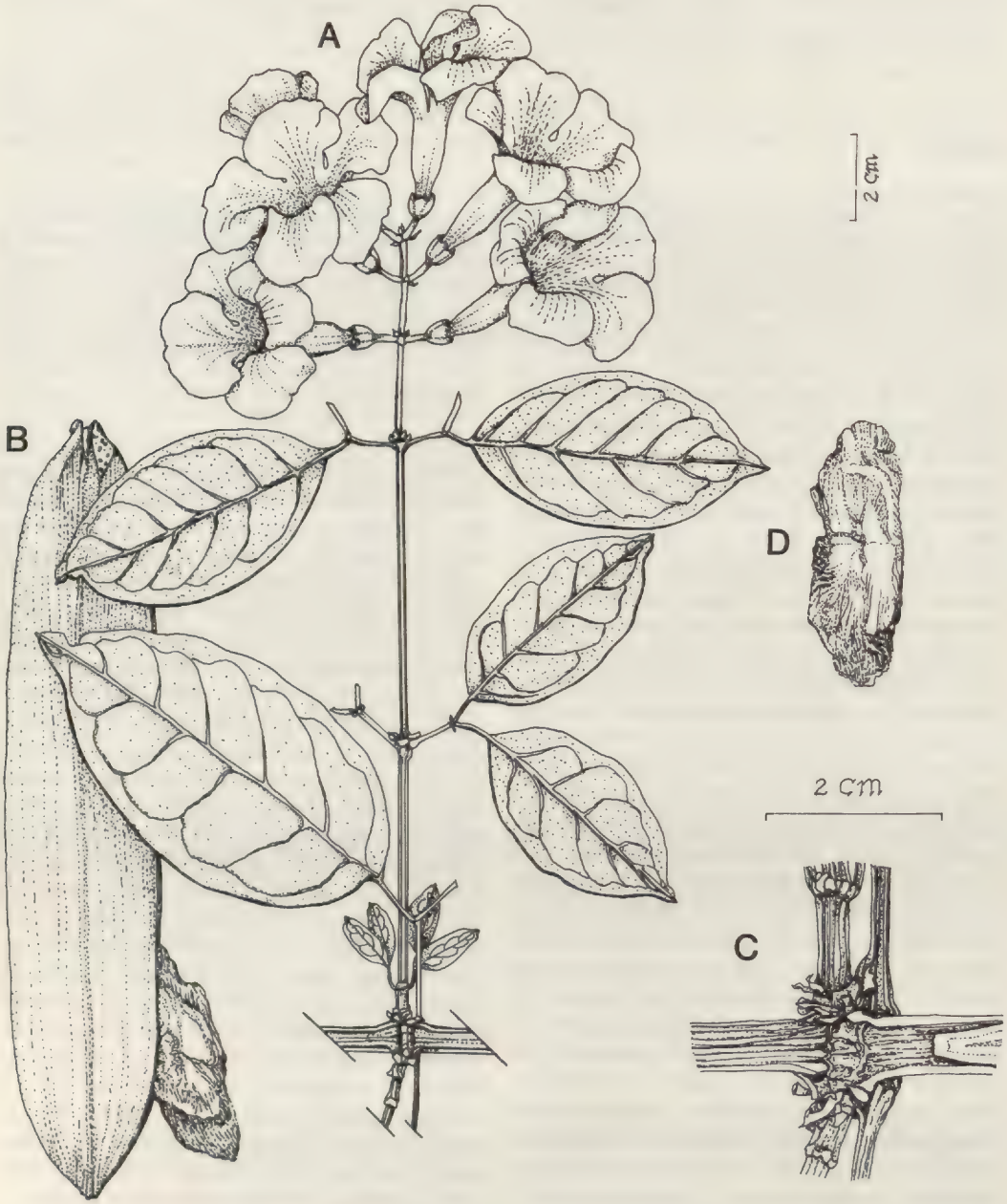


Figure 1. *Cydista potosina.* —A. Inflorescence and leaves after *C. Cowan 3022.* —B. Fruit with seed after *J. B. Alcorn 2172.* —C. Enlargement showing lateral branching and quadrangular stem. —D. Seed.

array of somewhat overlapping characters (Table 1; Gentry 1977a, 1997; Gentry & Tomb, 1979; Tomb & Gentry, unpublished). The genus most similar to *Cydista* is *Roentgenia,* which Gentry (1978) considered "barely separable from *Cydista.*" *Roentgenia* differs from *Cydista* in its trifid tendrils, racemose inflorescence, and colpate pollen according to the generic concepts established by Miers (1863) and Urban (1916), and later maintained by Macbride (1961) and Gentry (1977a, 1978, 1982). Gentry (1978) suggested that *Cydista lilacina* "links" the genera *Cydista, Roentgenia,* and *Clytostoma* by its elongate racemose-paniculate inflorescence and overall leaf appearance. *Clytostoma* differs from *Cydista* in its distinctive echinate fruit and glandular-warty ovary, although *Clytostoma* has a "*Cy-*

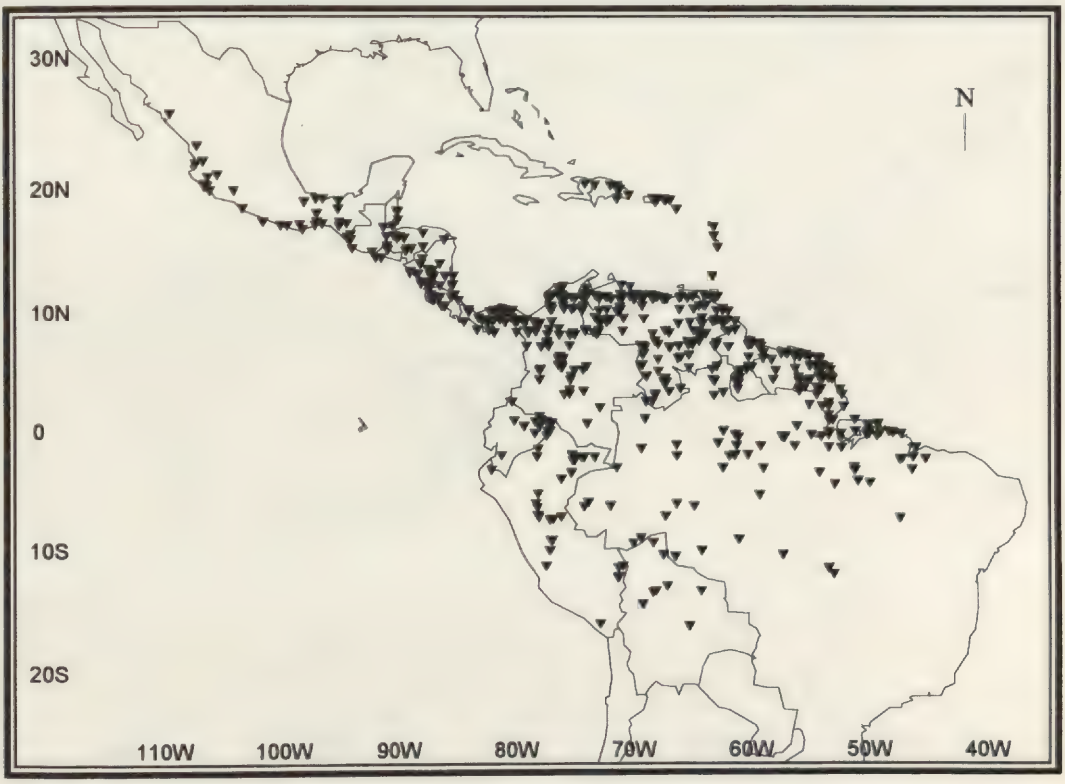


Figure 2. Distribution of *Cydista aequinoctialis* var. *aequinoctialis*.

dista-type" flower morphology (Gentry, 1978) and lacks a nectariferous disk. Gentry and Tomb (1979) suggested that the genera which lack a nectariferous disk and exhibit a tendency toward "multiple-bang" flowering phenologies (*Cydista, Roentgenia, Clytostoma,* and *Phryganocydia*) compose a natural group. All four genera possess glandular-lepidote corollas (Seibert, 1948; Gentry, 1977a), and *Cydista* and *Roentgenia* are characterized by conspicuous calyx glands (Seibert, 1948). Another closely allied genus is the monotypic *Potamoganos,* which shares the "*Cydista*-type" flower and cupular calyx, but lacks glandular fields and possesses a well-developed nectariferous disk (Gentry & Tomb, 1979).

Palynologically, *Cydista* species have medium-reticulate pollen (Gentry & Tomb, 1979), with pollen of *C. potosina* (K. Schum. & Loes.) Loes. and *C. heterophylla* inaperturate, that of *C. aequinoctialis* inaperturate or pericolpate, and that of *C. decora* (S. Moore) A. H. Gentry, *C. lilacina,* and *C. diversifolia* pericolpate. The latter three species may exhibit a pollen type intermediate to the colpate pollen of closely related genera (e.g., *Roentgenia*). *Clytostoma* shares with *Cydista* inaperturate, reticulate pollen but is distinguished by a medium to coarse-reticulate exine (Gentry & Tomb, 1979).

Goldblatt and Gentry (1979) reported chromosome counts of $2n = 40$ and $2n = 40 + 1\text{-}2B$ for *Cydista aequinoctialis.* The only other chromosome count reported for *Cydista* is $2n = 40$ for *C. diversifolia* (Venkatasubban, 1944). Based on a survey of 23 genera from tribe Bignonieae, these counts are consistent with a base number for the tribe of $x = 20$ (Goldblatt & Gentry, 1979).

Distribution

Cydista species are found primarily in lowland neotropical regions (Figs. 2–6) below 500 m in altitude, with collections reported from up to 2000 m for *C. aequinoctialis* and *C. diversifolia,* to 1200 m for *C. heterophylla,* to 950 m for *C. potosina,* to 900 m for *C. lilacina,* and to 3000 m for *C. decora.* Among *Cydista* species, *C. aequinoctialis* (var. *aequinoctialis*) is by far the most widely ranging (Fig. 2), extending from the western coast of Mexico through the southern West Indies to the eastern edge of Brazil and northern Paraguay. All other species are restricted to portions of this area. *Cy-*

Figure 3. Distribution of *Cydista aequinoctialis* var. *hirtella*.

dista potosina (Fig. 6) inhabits the southeastern half of Mexico and reaches central Nicaragua with a single collection known from southern Costa Rica. *Cydista heterophylla* (Fig. 5) has a range similar to that of *C. potosina*, except that it reaches the western coast of Mexico and extends through Panama into the northern coastal regions of Colombia. *Cydista diversifolia* (Fig. 4) has restricted representation along the coasts of central Mexico, is frequent in the Yucatán Peninsula and Cuba, and extends along the Pacific side of Honduras, Nicaragua, and Costa Rica, through Panama to central Colombia and northwestern and north-central Venezuela. The remaining two species, *C. decora* (Fig. 4) and *C. lilacina* (Fig. 6), are restricted almost exclusively to South America. *Cydista lilacina* is distributed throughout South America north of Paraguay. *Cydista decora* has a more restricted distribution than *C. lilacina* and inhabits two disjunct regions, one in western Ecuador and a second, larger area encompassing portions of Bolivia, Paraguay, and southwestern Brazil.

Phenology

Cydista aequinoctialis and *C. diversifolia* possess what Gentry (1974) referred to as "multiple-bang" flowering phenology. Multiple-bang species have numerous, synchronized, short flowering periods (ca. 3 days) that may occur at any time of the year. The absence of a nectariferous disk (and presumably nectar), coupled with conspicuous visual and olfactory attractants, indicates that pollinator deceit may be the ultimate pollination strategy. The short, repeated floral bursts may serve to lure novice pollinators that effect pollination through visits to only a few flowers, after which they seek a more ample nectar source. Visits by potential pollinators are infrequent, presumably because pollinators learn quickly that the flowers offer no nectar reward (Gentry, 1974).

Cydista heterophylla has a reduced multiple-bang flowering strategy with only a very few (1–2) bursts of flower production per year (Gentry, 1974). Detailed observations of flowering patterns in *C. lilacina*, *C. decora*, and *C. potosina* are not available.

Ethnobotanical and Economic Uses

Ethnobotanical reports include the use of *Cydista* branches for basket weaving in Mexico's Yucatán Peninsula, the incorporation of *C. ae-*

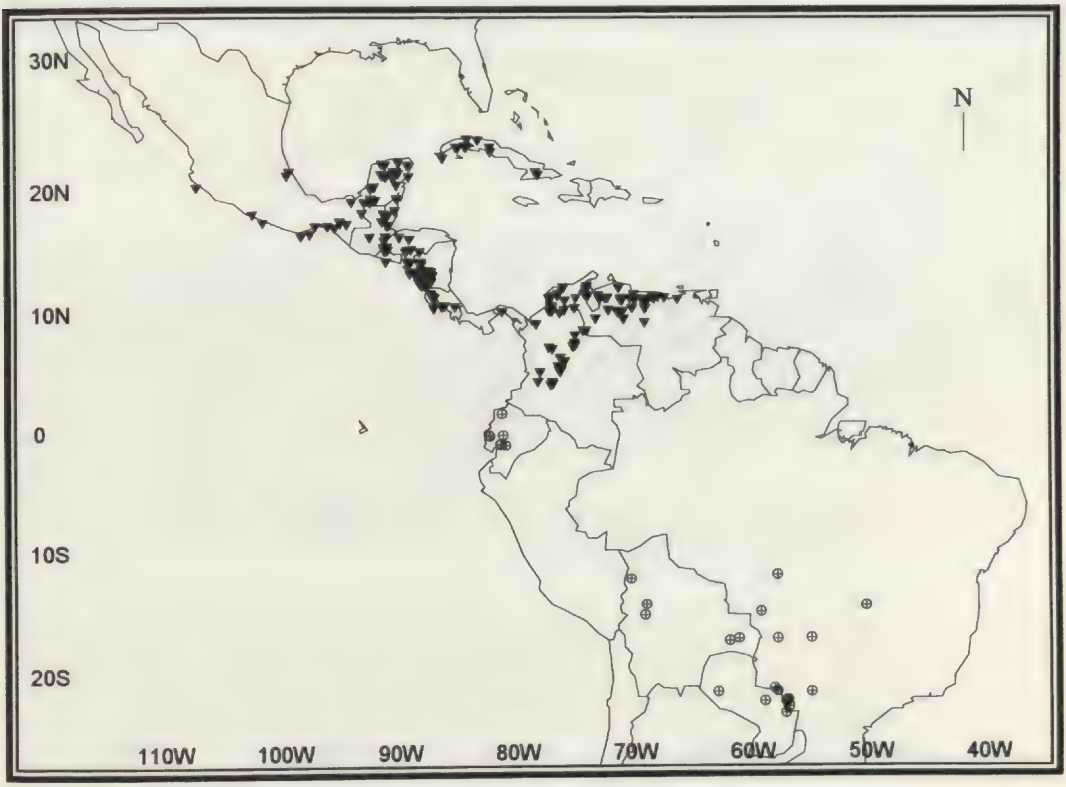


Figure 4. Distribution of *Cydista decora* (cross-circle) and *Cydista diversifolia* (triangle).

quinoctialis into an infusion used as eye drops, and the use of *Cydista* extracts to treat skin ailments and ringworm (Gentry, 1992). Bignoniaceae are known to produce naptho[1,2-b]furan and naptho[2,3-b]furan quinones, which have cytotoxic effects on neoplastic cells and exhibit potential utility as trypanosomicidal and virucidal agents (Ferreira et al., 1990).

Materials and Methods

Gentry established a private database that compiled label information from herbarium specimens he collected and from specimens that he personally examined at other herbaria. Gentry's private database has been incorporated into the Missouri Botanical Garden database management system TROPICOS, which now contains label information for all *Cydista* specimens housed at MO. For this treatment, all specimens entered into TROPICOS were assumed to have been examined by him. Specimens examined by the author are indicated by a "!" in superscript in the lists of representative specimens and the Index to Exsiccatae. All types were assumed to have been seen by Gentry unless otherwise noted. Only a single type, that of *C. lilacina*, was examined for this treatment. Gentry did not always designate types as "holotype," "isotype," or "syntype," and the designations presented here are based upon inferences drawn from Gentry's work and the original literature; these type designations were not based on personal verification of specimens at the various herbaria.

Data used for mapping and phenology were downloaded from TROPICOS. For records with no latitude/longitude coordinates in TROPICOS, coordinates were obtained from gazetteers produced by the U.S. Board on Geographic Names, Office of Geography, Dept. of the Interior. Distribution maps were produced using the computer program VERSAMAP 1.51 (C.H. Culberson, Newark, DE, 1991–1995). Graphs of flowering and fruiting phenology were generated using the computer program Quattro Pro 7.00 Corel Inc. (1996). Phenology is reported as the number of flowering specimens collected during each month of the year and does not imply that detailed studies of flower production (per plant, per population, per species, or per time period) have been conducted. Amounts of precipitation used in the graphs of phenology were obtained from *Agroclimatological Data for Latin America and the Caribbean* (FAO, 1985).

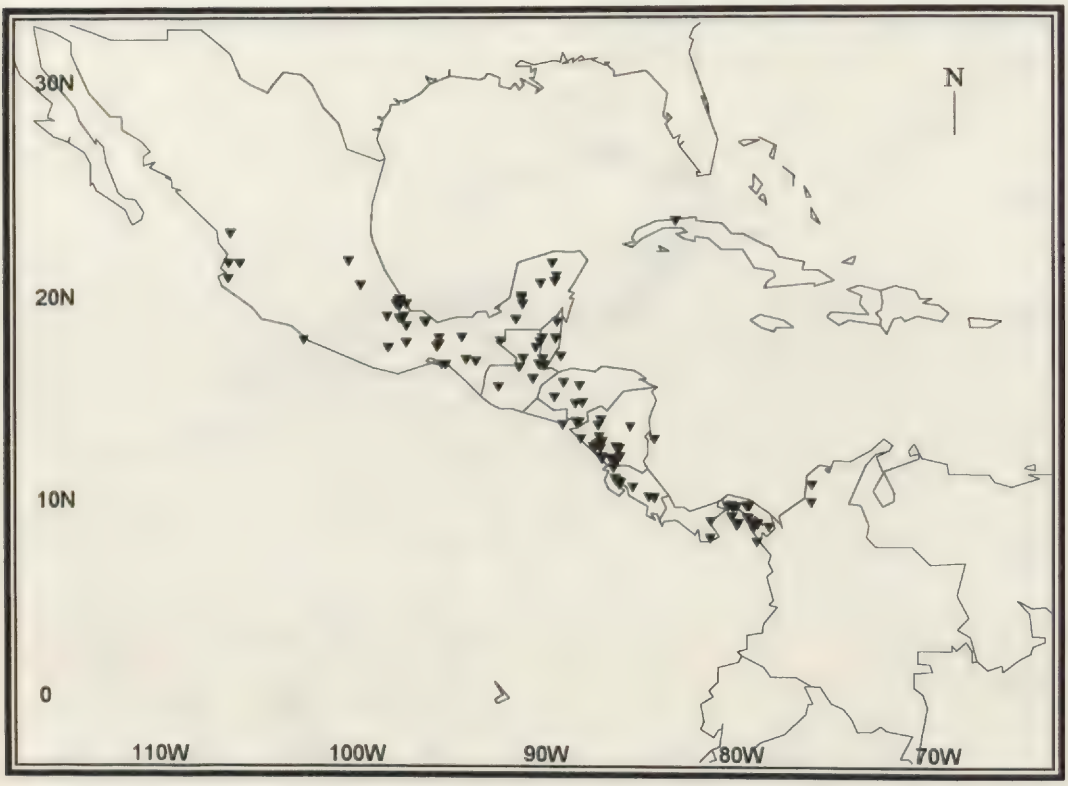


Figure 5. Distribution of *Cydista heterophylla.*

Taxonomic Treatment

Cydista Miers, Proc. Roy. Hort. Soc. London 3: 191. 1863. TYPE: *Cydista aequinoctialis* (L.) Miers.

Levya Bureau ex Baill., Hist. Pl. 10: 28. 1888. TYPE: *Levya nicaraguensis* Bureau ex Baill. = *Cydista aequinoctialis* var. *hirtella* (Benth.) A. H. Gentry.

Clytostomanthus Pichon, Bull. Soc. Bot. France 92: 224. 1945. TYPE: *Clytostomanthus decorus* (S. Moore) Pichon = *Cydista decora* (S. Moore) A. H. Gentry.

Lianas, stems woody with 8 phloem arms in cross section, branches terete to tetragonal, hollow or solid in cross section, interpetiolar glandular fields lacking, vegetative portions lepidote to puberulent; pseudostipules inconspicuous to foliaceous, generally eglandular. *Leaves* opposite, petiolate, estipulate, simple or 2(4)-foliolate with leaflets oppositely arranged, often with a simple, terminal tendril (or tendril scar); petioles and petiolules glabrate to conspicuously pilose or lepidote; leaflets entire, venation brochidodromous to actinodromous, secondary veins pinnate, midrib and secondary veins prominent, occasionally with glandular fields in axils, margins plane to slightly undulate. *Inflorescences* cymose, terminal or axillary, several- to many-flowered; rachis and peduncles minutely or conspicuously bracteolate. *Flowers* ovoid in bud, apices straight or curved; calyx campanulate, apically truncate, mucronate teeth present or absent, margin split or intact, eglandular, glabrate to densely lepidote; corolla conspicuously zygomorphic, campanulate-funnelform, white to pink or purple, glabrous to lepidote; corolla lobes 5 (2 upper and 3 lower), short-orbicular; fertile stamens didynamous, a single staminode present, stamen and staminode adnate to corolla; fertile anthers with two spreading thecae, included, glabrous; disk wanting, ovary cylindrical, usually densely lepidote, stigma bipartite, the divisions laterally flattened, included. *Fruit* a compressed, woody, elongate to elongate-linear septicidal capsule, valves parallel to the septum, midline inconspicuous, surface smooth to striate or wrinkled, glabrate to lepidote or puberulous, many-seeded; seeds oblong, flattened, bialate, occasionally subhyaline toward margin, body ovoid, frequently bipartite.

According to Gentry (1977a, 1982) there are six species and two varieties ranging from Mexico and

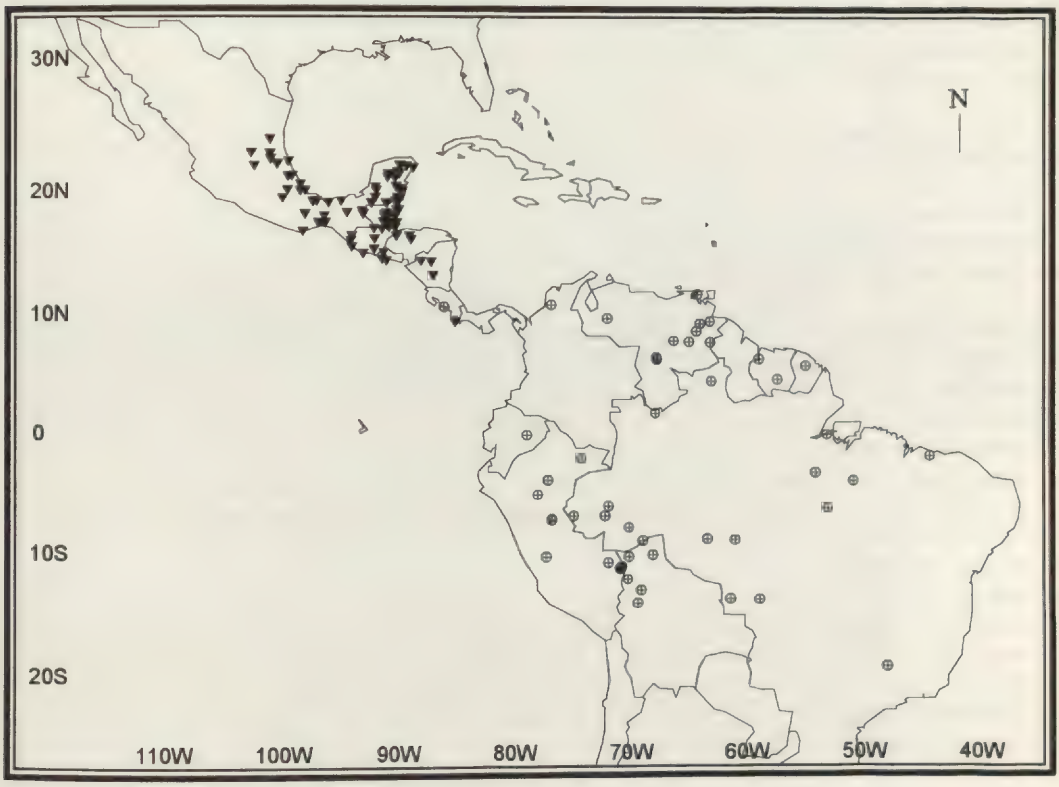


Figure 6. Distribution of *Cydista lilacina* (cross-circle) and *Cydista potosina* (triangle).

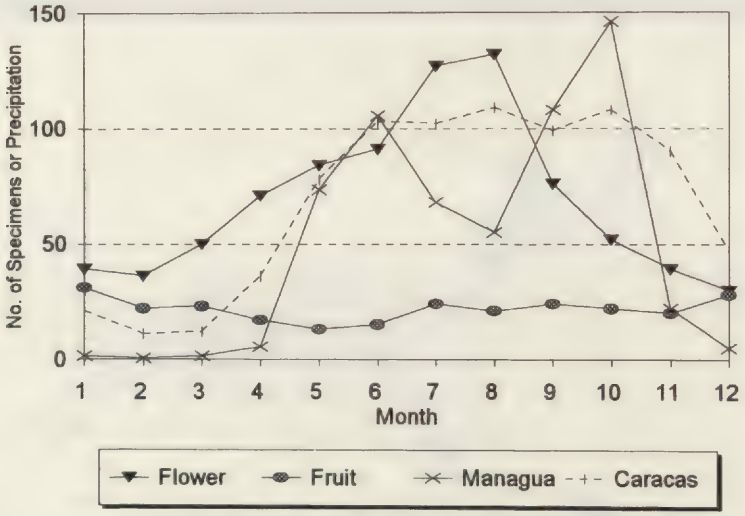
the West Indies through Central America to Brazil and Paraguay.

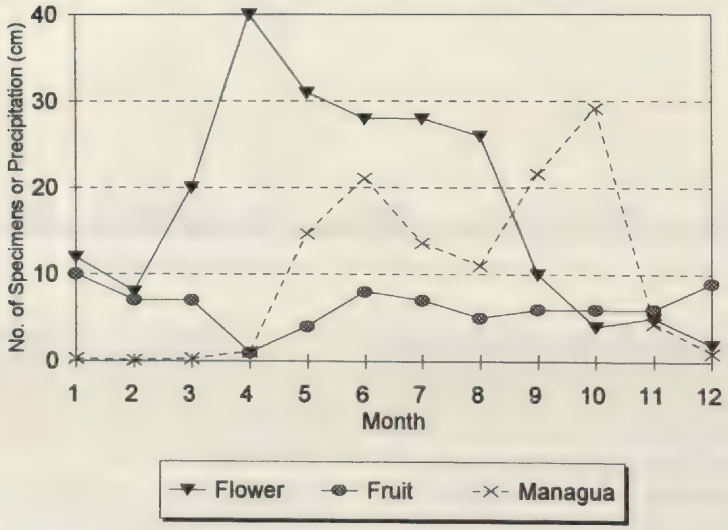
KEY TO FLOWERING SPECIMENS

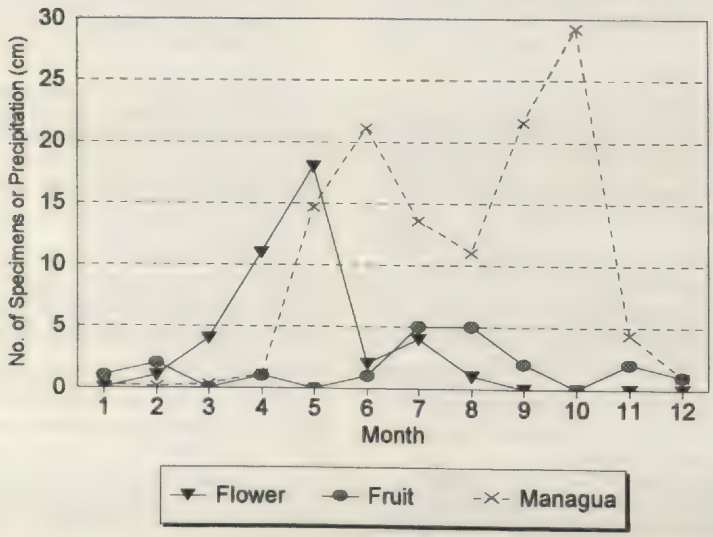
1. Calyces drying bicolorous apically, generally 2–5 mm long; pseudostipules linear-triangular, numerous, and overlapping ..... 6. *C. potosina*
1′. Calyces drying uniformly dark apically, generally 4–7 mm long; pseudostipules ovate-foliaceous or inconspicuous, paired, and never overlapping.
   2. Branchlets tetragonal; pseudostipules conspicuous and frequently foliaceous.
      3. Inflorescences conspicuously bracteate; branchlets solid in cross section ..... 2. *C. decora*
      3′. Inflorescences minutely bracteate; branchlets hollow in cross section ..... 3. *C. diversifolia*
   2′. Branchlets terete to subtetragonal; pseudostipules inconspicuous.
      4. Plants flowering while essentially leafless; glandular fields in axils of secondary veins infrequent and inconspicuous ..... 4. *C. heterophylla*
      4′. Plants flowering with leaves; glandular fields in axils of secondary veins frequent and (relatively) conspicuous.
         5. Older stems drying gray, younger stems drying dark; ovules 2-seriate; bud apices straight 1. *C. aequinoctialis*
         5′. Older and younger stems drying dark; ovules 4-seriate; bud apices curved ..... 5. *C. lilacina*

KEY TO FRUITING SPECIMENS

1. Capsules generally 3 cm wide or greater.
   2. Branchlets terete; capsule surface wrinkled; leaflets mostly 5–14 cm wide ..... 5. *C. lilacina*
   2′. Branchlets tetragonal; capsule surface smooth; leaflets mostly 2–5 cm wide ..... 6. *C. potosina*
1′. Capsules generally 2 cm wide or less.
   3. Branchlets hollow in cross section; capsule valves 1.0–1.5 cm wide; seed body darker than wings ..... 3. *C. diversifolia*
   3′. Branchlets solid in cross section; capsule valves generally 1.7–2.0 cm wide; seed body same color as wings.
      4. Pseudostipules conspicuous and foliaceous; branchlets tetragonal ..... 2. *C. decora*
      4′. Pseudostipules inconspicuous and poorly developed; branchlets terete to subtetragonal.
         5. Leaflets usually pinnately veined at petiole apex; fruit lacking submarginal ridges or margins inconspicuously raised ..... 1. *C. aequinoctialis*
         5′. Leaflets with 3 principal veins joined at petiole apex; fruit with 2 parallel submarginal ridges ..... 4. *C. heterophylla*


150
100
50
0
No. of Specimens or Precipitation
1 2 3 4 5 6 7 8 9 10 11 12
Month
Flower
Fruit
Managua
Caracas


40
30
20
10
0
No. of Specimens or Precipitation (cm)
1 2 3 4 5 6 7 8 9 10 11 12
Month
Flower
Fruit
Managua


30
25
20
15
10
5
0
No. of Specimens or Precipitation (cm)
1 2 3 4 5 6 7 8 9 10 11 12
Month
Flower
Fruit
Managua

1. **Cydista aequinoctialis** (L.) Miers, Proc. Roy. Hort. Soc. London 3: 191. 1863. *Bignonia aequinoctialis* L., Sp. Pl. 623. 1753. *Temnocydia aequinoctialis* (L.) Mart. ex DC., in A. DC., Prodr. 9: 155. 1845. TYPE: *Plumier,* Pl. Am., tab. 58 (holotype, P).

Lianas, older stems terete and drying gray, younger stems subtetragonal and drying dark often with four distinct light-colored ridges, solid in cross section, occasionally sparsely to densely lenticellate, glabrate to pilose; pseudostipules inconspicuous, lepidote. *Leaves* 11–21 cm long, once-pinnate with two primary leaflets and often a simple, terminal tendril; petioles 2–4 cm, lepidote or pilose; petiolules 1–4 cm, lepidote or pilose; leaflets entire, 7–14 × 3–7 cm, mostly narrowly to broadly ovate or ovate-elliptical, sometimes orbicular, apices acuminate to acute-acuminate, bases obtuse or rounded, occasionally oblique or inequilateral; venation actinodromous or brochidodromous basally, brochidodromous apically, 4–5 vein pairs, often with dark, abaxial confluent glandular fields in axils of secondary veins, veins glabrous or conspicuously pilose. *Inflorescences* to 14 cm long, several-flowered, peduncles 1.5–6.0 cm, the rachis and peduncles minutely bracteate, pedicels 5–18 mm long, sulcate, lepidote. *Flowers* ovoid in bud, apices straight; calyx 4–5 × 5–6 mm, drying uniformly dark, margin intact to shallowly split, teeth present and minute, lepidote with glandular fields apically or irregularly overall; corolla funnelform-campanulate, exserted 35 mm above level of calyx lip, 2–3 mm wide at calyx mouth, 15 mm wide at mouth, densely lepidote; corolla lobes 20–22 × 15 mm, irregularly elliptic-orbicular; stamens unequal, 9 or 15 mm long, shorter filaments inserted 3 mm and longer ones 8 mm above level of calyx lip, the staminode 3 mm long, inserted at level of calyx lip; ovary 3 mm long, lepidote, ovules 2-seriate, style 25 mm long. *Capsule* elongate-linear, 40–45 × 1.7–2.0 cm, submarginal ridges lacking or inconspicuous, the central ridge more prominent; seeds flattened, 1–2 × 3–4 cm, oblong with lateral membranous wings, each 2–2.5 cm long, hyaline margin 2 mm wide, body ovoid, 1 × 1.8 cm, bipartite, not well differentiated from wings. Figures: Schultz (1792: t. 81), Descourtilz (1822: t. 100), Rohrhofer (1931: t.3), and Gentry (Flora de Colombia ms., unpublished).

Cydista aequinoctialis is one of the most common and widely distributed species of the genus (Figs. 2, 3), extending from Mexico to Paraguay and eastern Brazil. It grows in tropical dry forests and in edaphically drier regions of tropical moist forests (Gentry, 1973b).

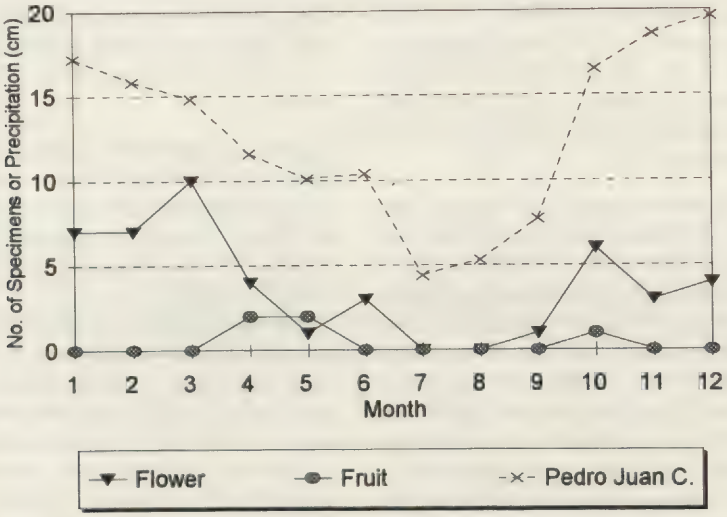
Morphologically *C. aequinoctialis* is the most variable of *Cydista* species. The leaflets range from narrowly to broadly elliptic, and venation varies from basally actinodromous to brochidodromous. Pollen in *C. aequinoctialis* varies from inaperturate to pericolpate and encompasses the range of pollen types in *Cydista.* Thus, *C. aequinoctialis* appears to be a cache for collections that do not fit clearly into the more narrowly defined limits of the other five species. A prominent field character is the presence of glandular fields in axils of main lateral veins on the undersurface of leaves (Gentry, 1973b), although these are not present on all collections and somewhat similar glandular fields can be observed on leaves of *C. lilacina.*

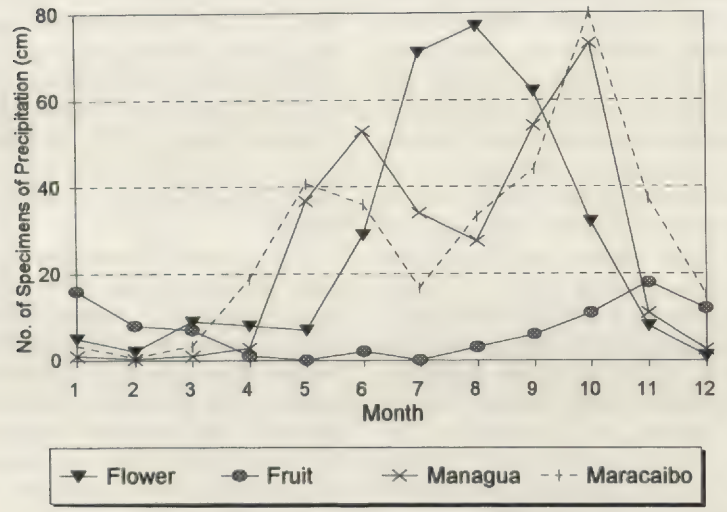
Two varieties of *C. aequinoctialis,* one with glabrate foliage and one with pubescent foliage, were recognized by Gentry (1973a), with "some hesitation as to the extent of genetic difference" between them. Gentry (1973a) reported that the glabrous and pubescent varieties grow in close proximity with otherwise identical features. A few individuals with intermediate pubescence are found. However, nearly all herbarium collections can be easily attributed to either the glabrous or pubescent variety. These two taxa appear to correlate with ecological parameters; the pubescent variety is found only in tropical dry forest, whereas the glabrous variety occurs in both tropical dry and moist forests, but more commonly in the latter (Gentry, 1973a). The two varieties have been recognized as distinct species under a number of different names.

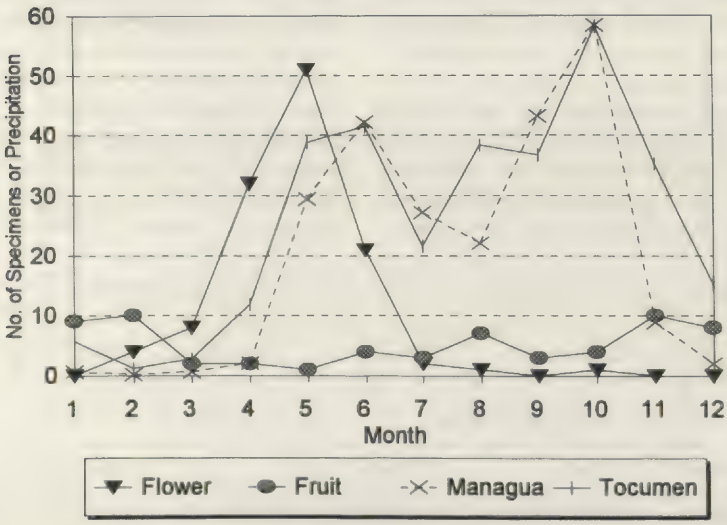
Gentry (1977a) noted that Plumier's illustrations were seen by Linnaeus in 1738.

←

Figures 7–9. Flowering and fruiting phenology. —Figure 7 (top). *Cydista aequinoctialis* var. *aequinoctialis,* for the entire range of the variety (see Fig. 2). Based on 827 flowering and 260 fruiting specimens. Precipitation in mm is plotted 0.5× for Managua, Nicaragua, and 1× for Caracas, Venezuela. —Figure 8 (middle). *Cydista aequinoctialis* var. *aequinoctialis,* from Central America. Based on 214 flowering and 82 fruiting specimens. Precipitation in cm is plotted for Managua, Nicaragua. —Figure 9 (bottom). *Cydista aequinoctialis* var. *hirtella.* Based on 41 flowering and 20 fruiting specimens. Precipitation in cm is plotted for Managua, Nicaragua.


No. of Specimens or Precipitation (cm)
20
15
10
5
0
1 2 3 4 5 6 7 8 9 10 11 12
Month
Flower
Fruit
Pedro Juan C.


No. of Specimens of Precipitation (cm)
80
60
40
20
0
1 2 3 4 5 6 7 8 9 10 11 12
Month
Flower
Fruit
Managua
Maracaibo


No. of Specimens or Precipitation
60
50
40
30
20
10
0
1 2 3 4 5 6 7 8 9 10 11 12
Month
Flower
Fruit
Managua
Tocumen

KEY TO VARIETIES OF *CYDISTA AEQUINOCTIALIS*

1. Leaflets glabrous or nearly so ..... 1A. *C. aequinoctialis* var. *aequinoctialis*
1'. Leaflets conspicuously pubescent, especially along main veins beneath ..... 1B. *C. aequinoctialis* var. *hirtella*

1A. Cydista aequinoctialis (L.) Miers var. aequinoctialis.

Bignonia spectabilis Vahl, Symb. Bot. 3: 80. 1794. *Cydista spectabilis* (Vahl) Miers, Proc. Roy. Hort. Soc. London 3: 191. 1863. *Temnocydia spectabilis* (Vahl) Mart. ex DC., in A. DC., Prodr. 9: 155. 1845. TYPE: collector unknown "ex India" (H. West?) (holotype?, C; isotype?, P-JU).

Bignonia villosa Vahl, Eclog. Amer. 2: 44. 1798. TYPE: Colombia. Santa Marta: *von Rohr 21* (holotype, C).

Bignonia picta Kunth, in Humb., Bonpl. & Kunth, Gen. Sp. Quarto ed. 3: 136, Folio ed. 3: 106. 1819. TYPE: Venezuela. Orinoco: *Humboldt & Bonpland 1078* (holotype, P).

Bignonia hostmannii E. Mey., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 12: 779. 1825. TYPE: Martinique. *Sieber s.n.* (isotypes?, M, W).

Bignonia nitidissima DC., in A. DC., Prodr. 9: 160. 1845. TYPE: Venezuela. Caracas: *Vargas 244* (holotype, G-DC).

Arrabidaea isthmica Standl., J. Wash. Acad. Sci. 15: 461. 1925. TYPE: Panama. Canal Zone: *Pittier 2576* (holotype, US; isotypes, GH, MO, NY).

Description as for *Cydista aequinoctialis* except younger stems, petioles, petiolules, veins of leaflets, and calyces glabrous or nearly so.

Although *Cydista aequinoctialis* var. *aequinoctialis* flowers throughout the year, the peak for all collections is July–August (Fig. 7). However, when the Central and South American collections are separated, two distinct peaks are observed: (1) Central American collections peak in April (Fig. 8), (2) South American collections climax during July–August. The differences in flowering collections in Central and South America may indicate that local populations have adapted to regional climatic patterns. Fruiting collections did not exhibit a marked peak, although Central American fruiting collections were most numerous from December to January.

Representative specimens. MEXICO. **Colima**: W of Manzanillo Bay, 5 mi. W of Santiago, 19°00'N, 104°00'W, 90–150 m, *McVaugh 15708* (MICH). **Guerrero**: Baqueta, *Langlassé 506* (F). **Jalisco**: Mun. La Huerta, Estación de Biología Chamela (UNAM), 19°30'N, 105°03'W, *Lott 1873* (MO[1]). **Nayarit**: 15 km SE of San Blas, near Miramar, 22°52'N, 105°06'W, 0 m, *Feddema 955* (MICH). **Oaxaca**: 12 km N de carretera Pinotepa–Pto. Escondido, Dtto. Jamiltepec, 16°17'N, 97°49'W, 0–3 m, *Torres & Cedillo 629* (MO[1]). **Sinaloa**: Villa Unión, Villa Unión, Mazatlán, 25°00'N, 107°30'W, 10 m, *González-Ortega 5448* (MEXU). **Tabasco**: 10–40 km W of Huimanguillo, Laguna Ocuapan, 17°51'N, 93°23'W, *Barlow 30/179* (MICH, WIS). **Veracruz**: Laguna de Sontecomapan–Río Coscompan, 1971, *Calzada 461* (CHAPA, F, MEXU, MO[1]). GUATEMALA. **Izabal**: Río Oscuro, 0–8 km SW of Lake Izabal, 14°05'N, 90°36'W, 0–600 m, *Jones & Facey 3491* (F, TEX-LL, MICH). **Petén**: Río Santa Isabel between El Porvenir & mouth of Río Sebol, 100 m, *Steyermark 45875* (F). **San Marcos**: Ocos, 14°31'N, 92°11'W, 1–2 m, *Steyermark 37855* (F). HONDURAS. **Colón**: road to Castillo, 0.2 mi. E Trujillo, 15°55'N, 86°00'W, *Saunders 170* (MO[1]). **Comayagua**: Las Limas, 14°08'N, 87°48'W, 1000 m, *Edwards P-128* (F). **Copán**: La Florida, *Pittier 8488* (US). **Cortés**: Entre Cofradia y Cusuco, 15°30'N, 88°00'W, 200–1300 m, *Molina 7299* (F, TEX-LL). **Gracias a Dios**: La Mosquitia, 15°00'N, 84°20'W, 1973, *Clewell & Cruz 4002* (MO[1]). **Morazán**: Cerca de Guaimaca, 14°30'N, 87°00'W, 800 m, *Molina 2800* (F). **Olancho**: Río Talgua, 14°45'N, 86°00'W, 400 m, *Molina 8310* (F). **Santa Bárbara**: Ulua River between Ilama and Gualala, 15°10'N, 88°20'W, 500 m, *Molina 22042* (F). BELIZE. **Belize**: 6–7 km NW of Belize, Northern Hwy., 17°30'N, 88°12'W, 1973, *Dwyer 10710* (MO). **Stann Creek**: 16°58'N, 88°13'W, *Schipp 771* (F, MICH, MO[1]). EL SALVADOR. **Ahuachapan**: El Imposible, San Benito al S del Río Arenal, 13°49'N, 89°56'W, *Sandoval & Chinchilla 332* (MO[1]). **Chalatenango**: Carretera a la Palma, 14°19'N, 89°11'W, *Montalvo & Vargas 3168* (MO). **Santa Ana**: *Vargas & Montalvo 3216* (MO[1]). NICARAGUA. **Chinandega**: Entre Corinto y Paso Caballos, 12°29'N, 87°10'W, *Sandino 2591B* (MO). **Chontales**: Río Mayales valley, near Cuapa, Llano Grande, 12°13'N, 85°25'W, 200 m, *Neill 7431* (MO[1]). **Estelí**: Salto la Estanzuela, 13°01'N, 86°21'W, 1000 m, *Moreno 21153* (MO[1]). **León**: Km 55 carretera Nueva a León, 12°18'N, 86°42'W, 40–60 m, *Moreno 9870* (MO[1]). **Managua**: road between El Crucero and house of Finca Santa Julia, 11°59'N, 86°19'W, 600–900 m, *Standley 8381* (F). **Matagalpa**: Las Palomas, 11 km al SW de Río Blanco, Matiguas, 12°52'N, 85°15'W, *Moreno 23962* (MO). **Nueva Segovia**: Mun. El Jícaro, 8 km NE del Jícaro, 13°45'N, 86°06'W, *Moreno 1693* (MO). **Río San Juan**: San Miguelito, 11°23'N, 84°54'W, 50–80 m, *Sandino & Martínez 3868* (MO). **Rivas**: Isla Ometepe, Volcán Concepción, 11°32'N, 85°34'W, 50 m, *Robleto 1594* (MO[1]). **Zelaya**: Harbor of Bluefields, 12°00'N, 84°10'W, *Marshall & Neill 6522* (MO[1]). COSTA RICA. **Alajuela**: San Mateo, 09°56'N, 84°31'W, *Brenes 3647* (CR, F, NY). **Guanacaste**: Finca la Pacifica, 2–3 mi. N of Cañas, 10°26'N, 85°06'W, *Gentry 1113* (F, MO). **Limón**: Cerro Coronel, along Río Colorado at Laguna Danto, 10°42'N, 83°39'W, 7 m, *Stevens 24012* (MO). **Puntar-**

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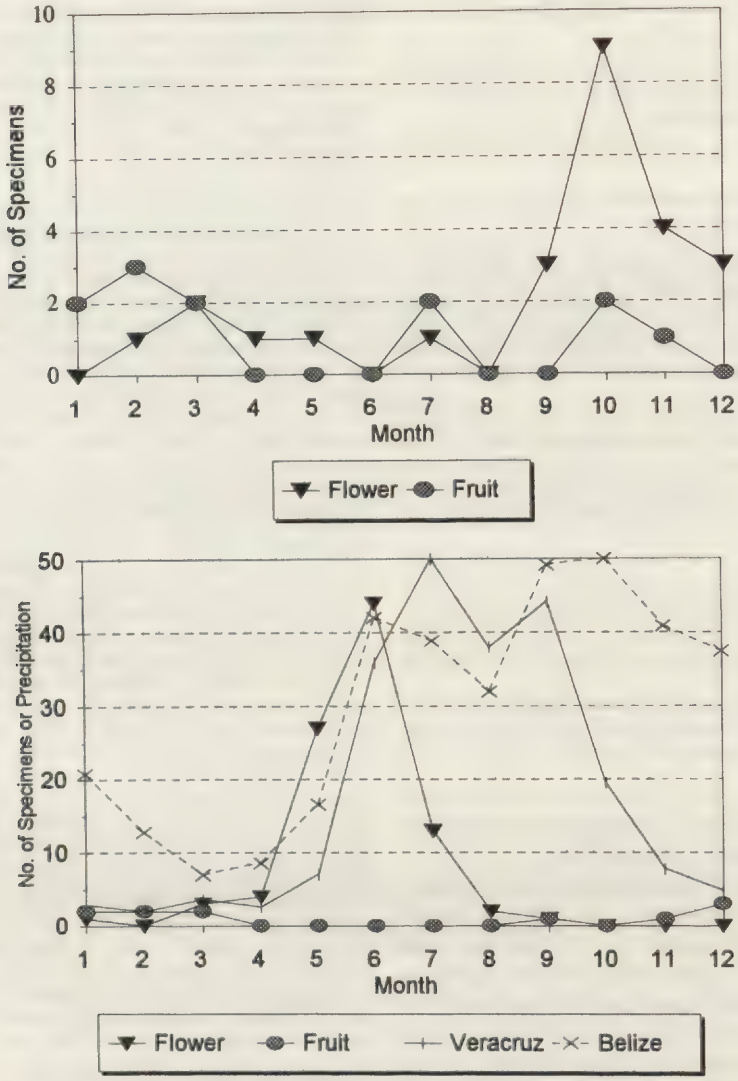
Figures 10–12. Flowering and fruiting phenology. —Figure 10 (top). *Cydista decora*. Based on 46 flowering and 5 fruiting specimens. Precipitation in cm is plotted for Pedro Juan Caballero, Paraguay. —Figure 11 (middle). *Cydista diversifolia*. Based on 311 flowering and 84 fruiting specimens. Precipitation in cm is plotted for Managua, Nicaragua, and Maracaibo, Venezuela. —Figure 12 (bottom). *Cydista heterophylla*. Based on 120 flowering and 63 fruiting specimens. Precipitation in mm is plotted 0.2× for Managua, Nicaragua, and 0.17× for Tocumen, Panama.



Figures 13, 14. Flowering and fruiting phenology. —Figure 13 (top). *Cydista lilacina*. Based on 25 flowering and 12 fruiting specimens. —Figure 14 (bottom). *Cydista potosina*. Based on 95 flowering and 11 fruiting specimens. Precipitation in cm is plotted 1.25× for Veracruz, Mexico, and 0.2× for Belize, Belize.

Table 1. Morphological/anatomical characters and character states for *Cydista* and four genera that are presumably closely related (after Gentry, 1977a, 1997; Gentry & Tomb, 1979; Tomb & Gentry, unpublished).

	Tendrils	Phloem arms	Nectar disk	Corolla pubescence	Ovule organization	Fruit surface	Seed	Pollen aperture	Pollen exine
Cydista	simple	8	absent	lepidote	2(–4)-seriate	smooth	bialate	inaperturate/ pericolpate	reticulate
Roentgenia	bi-trifid	8	absent	lepidote	2-seriate	smooth	bialate	3(–4)-colpate	reticulate
Phryganocydia	simple	8	absent	lepidote	2-seriate	smooth	corky	inaperturate	reticulate
Clytostoma	simple	8	absent	lepidote	2(–4)-seriate	echinate	corky	inaperturate	reticulate
Potamoganos	trifid	4	present	glabrous/ lepidote	4-seriate	?	?	3-colpate	reticulate

enas: Osa Peninsula near Rincón, 09°55′N, 84°13′W, *Gentry 1263* (MO). **San José**: Tabarcia, Bajo de los Bustamante, 09°51′N, 84°14′W, 840 m, *Solís 543* (CR-24222). PANAMA. **Bocas del Toro**: Río San Pedro, 08°49′N, 81°33′W, *Gordon 80C-a* (MO[1]). **Canal Zone**: Barro Colorado Island, 09°11′N, 79°57′W, *Croat 11097* (SCZ). **Chiriquí**: Puerto Armuelles, 08°17′N, 82°52′W, *Croat 25036* (MO[1]). **Coclé**: vicinity of El Valle, 08°37′N, 80°08′W, 600–1000 m, *Allen 1780* (F, GH, MO[1], NY, US). **Colón**: along roadside ca. 2 mi. E of Fort Sherman, 09°22′N, 79°57′W, *Gentry 733* (MO[1]). **Darién**: El Real, 08°08′N, 77°43′W, *Gentry 4564* (MO[1]). **Herrera**: 0.5 mi. E of Las Minas, 07°48′N, 80°45′W, *Gentry 3138* (MO[1]). **Los Santos**: Punta Mala, 07°28′N, 80°00′W, *D'Arcy & Croat 4215* (MO[1]). **Panamá**: Tocumen, 09°01′N, 79°23′W, *Dwyer 5130* (MO). **San Blas**: mountains above Puerto Obaldía, 08°40′N, 77°25′W, *Gentry 1477* (MO). **Veraguas**: Islas Contreras, Islo Brincaneo, 07°51′N, 81°47′W, 0 m, *Churchill 5711* (MO[1]).

HAITI. Bayeux, Bord-de-la-mer, 19°49′N, 72°26′W, *Ekman H2669* (MO[1]). DOMINICAN REPUBLIC. **Distrito Nacional**: Arroyo Tosa, 1.5 km from La Victoria on road to Mata Mamon, 18°36′N, 69°50′W, 10–20 m, *Mejía & Zanoni 9017* (MO[1]). **El Seibo**: Laguna El Limón, 38 km E of Miches, 18°58′N, 68°51′W, 0–5 m, *Zanoni et al. 15883* (JBSD, MO). **Espaillat**: 8 km W de Gaspar Hernández, 19°38′N, 70°10′W, 10 m, *Gentry & Zanoni 50609* (MO). **María Trinidad Sánchez**: Llanura de Nagua, 29.4 km al NW de Nagua, 19°33′N, 69°55′W, 20–30 m, *Mejía & Pimentel 23630* (JBSD, MO). **Samaná**: en las orillas del Río Gran Estero, 13 km sureste de Nagua, 19°16′N, 69°46′W, *Zanoni et al. 30037* (MO). PUERTO RICO. Mun. of Fajardo, 1 km E of route 3, 18°17′N, 65°38′W, 30 m, *Miller & Sherman 6480* (MO); Guaynabo, Bo. San Patricio, 18°22′N, 66°06′W, *Otero 570* (MO[1]). U.S. VIRGIN ISLANDS. **St. Croix**: 17°45′N, 06°45′W, *Benson 151-4124* (C). **St. Thomas**: Magens Bay, 18°17′N, 64°99′W, *Eggers 310* (FI, L). GUADELOUPE. 16°01′N, 61°31′W, *Isert s.n.* (C). DOMINICA. Coastal road between Batali River and Coulibistri, 15°30′N, 61°28′W, 0 m, *Ernst 1395* (MO). GRENADA. W. Ind. Woburn, 12°02′N, 61°44′W, *Broadway 1004* (L). MARTINIQUE. Environs de la case Pilote Mars, 14°35′N, 61°00′W, *Hahn 1407* (MICH). TRINIDAD AND TOBAGO. **Trinidad**: entrance to Caroni Swamp National Park, near Port of Spain, 10°32′N, 61°30′W, *Harriman 17563* (MO).

COLOMBIA. **Amazonas**: Leticia, 04°09′S, 69°57′W, 1974, *Gentry 12735* (COL, MO[1]). **Antioquia**: Mun. de Sabanalarga, 8 km de Sabanalarga, 06°51′N, 75°49′W, 1100 m, *Callejas et al. 2238* (MO[1]). **Atlántico**: Barranquilla Las Delicias, 10°58′N, 74°54′W, 1937, *Dugand 1135* (F, MO[1]). **Bolívar**: near Cartagena, 10°28′N, 75°32′W, 10 m, *Gentry & Cuadros 47618* (MO). **Boyacá**: El Yopal, Llanos Orientales, 04°44′N, 72°15′W, *Blydenstein & Saravia 1251* (COL). **Caldas**: 14–21 km N of La Dorada on road to San Miguel, 05°27′N, 74°40′W, 330 m, *Gentry et al. 18150* (COL, MO!). **Caquetá**: Cuernan, Río Caquetá, *Pabon 533* (ARAR). **Cesar**: 5 km W of Manaure, 10°22′N, 73°08′W, 440–460 m, *Gentry et al. 60737* (JBGP, MO). **Chocó**: Ríosucio, Parque Natural Nacional Los Kaytos Cacaricas, 07°25′N, 77°10′W, 120 m, *León 338* (COL, MO[1]). **Córdoba**: road from Fresquillo to Tierralta, 08°05′N, 76°10′W, 100 m, *Gentry & Cuadros 63956* (MO). **Cundinamarca**: 4 km W of La Mesa towards Tocaima, 04°38′N, 74°28′W, 900 m, *Gentry 15149* (COL, MO[1]). **Guainía**: San Felipe, 01°47′N, 67°06′W, 120 m, *Gentry & Stein 46475* (MO[1]). **Guaviare**: San José del Guaviare, 02°35′N, 72°38′W, 240 m, *Cuatrecasas 7473* (COL). **Magdalena**: Parq. Nac. Tairona, 50 m, *Gentry & Cuadros 47502* (JBGP, MO). **Meta**: Mun. La Macarena, Río Guayabero 02°10′N, 74°06′W, 310 m, *Callejas & Marulanda 7118* (MO[1]). **Nariño**: Tumaco, Mun. Espriella, 01°49′N, 78°46′W, *Romero-Castañeda 2793* (COL). **Norte de Santander**: Río del Oro, 09°09′N, 72°50′W, 40–50 m, *García-Barriga & Lozano 18271* (COL, MO). **Santa Cruz**: 5 km WNW of Buena Vista, 17°27′S, 63°42′W, 350 m, *Nee et al. 36128* (MO). **Santander**: 51 km E of Barranca Bermeja toward Bucaramanga, 07°03′N, 73°52′W, 200 m, *Gentry & Forero 15351* (MO[1]). **Sucre**: Coloso to Finca Sirena, along Quebrada El Salto, 09°30′N, 75°21′W, 300 m, *Gentry & Cuadros 68250* (MO[1]). **Tolima**: Mariquita, 05°12′N, 74°54′W, 600–650 m, *Uribe-Uribe 3003* (COL). **Valle**: Armenia turnoff from Cali–Medellín hwy., S of Zarzal, 04°25′N, 76°05′W, 1000 m, *Gentry & Juncosa 40922* (MO[1]). **Vaupés**: Río Kananari, Cachoera Palito, *Schultes & Cabrera 13126* (COL). **Vichada**: near Humaypia, Río Vichada, 04°55′N, 67°50′W, *Giovanni s.n.* (COL). ECUADOR. **Napo**: 2–6 km above Puerto Bolívar, Río Cuyabeno, 00°06′S, 76°10′W, 300 m, *Brandbyge et al. 33731* (AAU, MO[1]). **Pastaza**: Via Auca, 115 km al S de Coca, cerca del Río Tiguino, 01°15′S, 76°55′W, 320 m, *Rubio 121* (MO[1]). **Sucumbíos**: Cuyabeno, 00°16′S, 75°53′W, 265 m, *Paz & Mino 81001* (MO[1]). PERU. **Junín**: Chanchamayo Province, Hacienda La Genoa, Finca Italia, 11°05′S, 75°25′W, 1150 m, *Gentry et al. 73439* (MO). **Loreto**: Requena, Sapuena, Jenaro Herrera, 04°50′S, 73°45′W, 170 m, *Vásquez et al. 10040* (MO[1]). **Madre de Dios**: Tambopata, ca. 5 km from Puerto Maldonado, 12°35′S, 69°09′W, 200 m, *Gentry & Revilla 16281* (MO). **Pasco**: Cabeza de Mono, Río Iscozacin, 10°20′S, 75°18′W, 320 m, *Gentry et al. 41685* (MO). **Puno**: Río Tavara, ridge top across from mouth of first major tributary, 13°21′S, 69°40′W, 500 m, *Gentry et al. 76897* (MO[1]). **San Martín**: Tocache Nuevo, 08°10′S, 76°32′W, 450 m, *Gentry et al. 25480A* (MO[1]). **Ucayali**: Coronel Portillo, Bosque Nacional de von Humboldt, 08°40′S 75°00′W, 270 m, *Gentry & Horna 29508* (MO[1]). BOLIVIA. **Beni**: Yacuma, San Borja, 50 km hacia San Ignacio de Mojos, 14°49′S, 66°51′W, 250 m, *Beck 13215* (MO[1]). **La Paz**: Alto Beni, 14°00′S, 65°30′W, *Seidel & Schulte 2324* (MO[1]). **Pando**: Abuna Province, Nuevo Mundo, Campamento 18, 18 km N of airstrip, 10°39′S, 66°46′W, 160 m, *Gentry et al. 77759* (MO). **Santa Cruz**: Perseverancia, NW of Santa Cruz on Río Negro, 14°38′S, 62°37′W, 100 m, *Gentry & Mostacedo 73715* (MO[1]). VENEZUELA. **Amazonas**: banks of the Río Manapiare, close to San Juan de Manapiare, 05°04′N, 66°03′W, *Berry 1593* (MO[1]). **Anzoátegui**: km 227 on Caracas–Barcelona Hwy., 16 km E of Boca de Uchire, 10°08′N, 65°26′W, *Gentry & Berry 14833* (MO[1]). **Apure**: Dtto. San Fernando, 06°16′N, 67°31′W, 55 m, *Davidse & González 14363* (MO[1]). **Aragua**: 8–9 km from the redoma at Cata Beach, SW towards Cuyaga, 10°29′N, 68°42′W, 400 m, *Holst et al. 2289* (MO[1]). **Barinas**: 10–15 km W of Barinas, 08°38′N, 70°12′W, *Gentry & Puig-Ross 14263* (MO[1]). **Bolívar**: Mun. Piar. Isla en el lago de Guri, 07°35′N, 62°58′W, 270 m, *Aymard et al. 10301* (MO[1]). **Carabobo**: Bahiá de Patanemo, 10°26′N, 67°55′W, *Delascio Chitty 2417* (MO[1]). **Delta Amacuro**: Dept. Pedernales, Cano Angosturita, 09°52′N, 62°03′W, 50 m, *Steyermark et al. 114300* (MO[1]). **Distrito Federal**: La Guaira, Est. Teleferico del Avila, 10°36′N, 66°56′W, *Plowman 7664* (MO[1]). **Falcón**: Dtto. Zamora, Cerro

Mampostal, 11°27′N, 69°17′W, 400 m, *González 1051* (MO[1]). **Guárico**: banks of Río Orituco, S of Calabozo, 08°45′N, 67°27′W, *Gentry 10263* (MO[1]). **Lara**: Jiménez Parq. Nac. Yacambu Qda. Honda, 09′41°N, 69°30′W, 700 m, *Davidse & González 21329* (MO[1]). **Mérida**: Santa María de Caparo, Dtto. Arzobispo Chacón, 08°30′N, 71°10′W, *López-Palacios & Bautista 3299* (MO[1]). **Miranda**: Cerros del Bachiller, 10 km of Cupira, 10°09′N, 65°48′W, *Steyermark & Davidse 116368* (MO[1]). **Monagas**: Río San Juan, Dtto. Benítez, Estado Sucre y Dtto. Maturin, Monagas, 09°24′N, 63°02′W, *Marcano-Berti 77-1-76* (MO[1]). **Portuguesa**: Dtto. Guanare. Colonia Agrícola, 09°07′N, 69°53′W, 200 m, *Aymard & Cuello 3566* (MO[1]). **Sucre**: Dtto. Benítez, E of Los Pozotes, 10°30′N, 63°07′W, *Steyermark et al. 121268* (MO[1]). **Táchira**: Dtto. Capacho, 07°52′N, 72°19′W, 1250 m, *Bono 4950* (MO[1]). **Trujillo**: Sabana Libre, 09°21′N, 70°39′W, *Christ 75* (VEN). **Zulia**: Dtto. Perijá, Carretera San Ignacio–Barranquitas, 10°00′N, 72°30′W, 125–150 m, *Bunting 5460* (MO[1]). GUYANA. **Demerara**: Demerara–Mahaica Region, along road from Cane Grove to Lamay Conservancy, 06°35′N, 57°50′W, 1–10 m, *Hahn et al. 3817* (MO[1]). **Essequibo**: W Demerera Region, W of Demerara River, 06°40′N, 58°11′W, 1 m, *Pipoly & Ameer 9110* (MO[1]). SURINAME. **Commewijne**: Zwamp, 140 m ten Noorden van Visserijzwamp, 05°01′N, 5°42′W, *Reijenga 57* (U). FRENCH GUIANA. **Cayenne**: Riviere de Kaw, 04°48′N, 52°09′W, *Granville 6848* (MO[1], U). **Inini**: Riviere Grand Inini, en amont de Saut Badjere, 04°39′N, 52°20′W, *Granville B-3728* (CAY, MO[1]). **Saül**: 03°38′N, 53°12′W, 220 m, *Gentry et al. 62974* (MO).

1B. Cydista aequinoctialis var. **hirtella** (Benth.) A. H. Gentry, Ann. Missouri Bot. Gard. 60: 838. 1973. *Bignonia sarmentosa* Bertol. var. *hirtella* Benth., Bot. Voy. Sulphur 128. 1845. TYPE: Nicaragua. Realejo: *Hinds s.n.* (isotype?, K).

Bignonia sarmentosa Bertol., Fl. Guatimal. 25. 1840. *Cydista sarmentosa* (Bertol.) Miers, Proc. Roy. Hort. Soc. London 3: 191. 1863. TYPE: Guatemala. Esquintla: *Velásquez s.n.* (holotype?, BOLO).

Levya nicaraguensis Bureau ex Baill., Hist. Pl. 10: 28–29. 1888. TYPE: Nicaragua. *Levy 38* (holotype?, P; isotypes?, F, K).

Arrabidaea guatemalensis K. Schum. & Loes., in Loes., Bot. Jahrb. Syst. 23: 129. 1896. TYPE: Guatemala. *Bernoulli & Cario 2056* (holotype, K).

Arrabidaea pseudochica Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 19. 1921. (fide Sandw., Kew Bulletin 22: 403–420. 1960.) TYPE: Mexico. Michoacán: *Langlassé 137, 506* (syntypes, K).

Anemopaegma tonduzianum Kraenzl., Repert. Spec. Nov. Regni Veg. 17: 116. 1921. TYPE: Costa Rica. Guanacaste: *Tónduz 13912* (isotypes?, K, P).

Cydista pubescens S. F. Blake, Contr. U. S. Natl. Herb. 24: 23. 1922. TYPE: Honduras. Copán: *Pittier 8488* (holotype?, US).

Description as in *C. aequinoctialis* except that the younger stems, petioles, petiolules, and veins of leaflets are conspicuously pilose.

Variety *hirtella* is restricted primarily to Mexico and Central America (Fig. 3); only three collections are known from South America. The number of flowering specimens of *C. aequinoctialis* var. *hirtella* peaks in May (Fig. 9), whereas in variety *aequinoctialis* the peak is April (Fig. 8). Both varieties initiate flowering before the onset of the wet season in May, but flowering collections of variety *hirtella* drop sharply after May, and flowering collections of variety *aequinoctialis* remain common through August. These apparent differences in phenology may be a consequence of ecological diversification (Gentry, 1973a). However, few stable characters are available to distinguish the two varieties, and recognition at a higher taxonomic rank is not warranted at this time.

Representative specimens. MEXICO. **Chiapas**: Acala, *Laughlin 850* (DS, F, MEXU). **Guerrero**: Montes de Oca, Vallecitos, *Hinton 10219* (MO[1]). **Oaxaca**: 5 km N of Matias Romero, *King 808* (MICH). **Santiago**: Pinotepa, 16°19′N, 98°01′W, *Galeotti 7060E* (MO). **Veracruz**: Estación de Biología Tropical Los Tuxtlas, 18°34′N, 95°09′W, 450 m, *Colín 144* (MO[1]). GUATEMALA. **Jutiapa**: Río Paz, *Heyde 6363pp* (MO). HONDURAS. **Comayagua**: Humuya River, *Hazlett 1099* (MO). EL SALVADOR. **Ahuachapán**: 0–2 mi. NE of San Francisco Menéndez, 200–450 m, *Croat 42068* (MO[1]). NICARAGUA. **Carazo**: between Amayito and Barranco, 11°40′N, 86°18′W, 30–300 m, *Stevens 22734* (MO[1]). **Chontales**: 0.6 km NE of Hwy. 7 on road to Comalpa, 12°10′N, 85°33′W, 160 m, *Stevens et al. 17177* (MO[1]). **Estelí**: Paso León, 3.9 km NNE of Hwy. 1 at Estelí, 13°08′N, 86°20′W, 815 m, *Stevens et al. 15487* (MO[1]). **León**: 4.0 SW of La Paz Centro, 12°18′N, 86°42′W, 35 m, *Stevens et al. 17243* (MO[1]). **Matagalpa**: carretera vieja a Jinotega, 800 m, *Moreno 22917* (MO[1]). **Nueva Segovia**: El Jícaro, 13°45′N, 86°06′W, 650–700 m, *Moreno 1693* (MO[1]). **Rivas**: Potrero Largo, 11°05′N, 85°42′W, 10–20 m, *Morales 2935* (MO[1]). **Rio San Juan**: San Miguelito, *Sandino & Martínez 3868* (MO[1]). COSTA RICA. **Guanacaste**: Isla San José, 10°53′N, 85°55′W, 50 m, *Janzen 12474* (MO[1]). PANAMA. **Darien**: Golfo de San Miguel, *Gentry 3957* (MO[1]). **Veraguas**: ca. 11 mi. W of Sorá, *D'Arcy 5279* (MO[1]).

COLOMBIA. **Chocó**: Bahia Solano, *Gentry & Fallen 17173* (MO[1]). **Santander**: Los Santos, Sabana de Torres, 328 m, *Renteria 202* (MEDEL). VENEZUELA. **Zulia**: 13 km N de Embalse, 10°25′N, 70°49′W, 550–600 m, *Bunting et al. 11268* (MO[1]).

2. Cydista decora (S. Moore) A. H. Gentry, Selbyana 2: 42. 1977. *Anemopaegma decorum* S. Moore, Trans. Linn. Soc. London, Ser. 2. 4: 421. 1895. *Clytostoma decorum* (S. Moore) Bureau & K. Schum., in Mart., Fl. Bras. 8c: 151. 1896. *Arrabidaea decora* (S. Moore) Hassl., Spec. Nov. Regni Veg. Repert. 9: 49. 1910. *Clytostomanthus decorus* (S. Moore) Pichon, Bull. Soc. Bot. France 92: 224. 1945. TYPE: Brazil. Mato Grosso: *S. Moore 980* (holotype, BM; isotype, NY).

Lianas, stems tetragonal with four conspicuous

ridges, solid in cross section, drying gray to brown, glabrous; pseudostipules foliaceous, 2.5 × 2.0 cm, elliptic-orbicular, entire, glabrous. *Leaves* 8–13 cm long, bifoliolate with a simple, terminal tendril (or tendril scar); petioles 2–4 cm, sulcate, glabrate to puberulent, petiolules 1–4 cm, sulcate, glabrate to puberulent; leaflets 6–9 × 3–7 cm, mostly narrowly to broadly ovate or ovate-elliptical, apices acute to acute-obtuse, bases obtuse or rounded, occasionally oblique, venation actinodromous basally and brochidodromous apically, 4–5 vein pairs, midrib and secondaries prominent, major veins puberulous beneath, isolated and scattered glands often in axils of secondary veins, margins slightly undulate, chartaceous. *Inflorescences* to 20 cm long, several-flowered, peduncles 3.0–7.5 cm, the rachis and peduncles conspicuously bracteate, the bracts 2–10 mm long, pedicels 5 mm long, sparsely lepidote, puberulent. *Flowers* ovoid in bud, apices straight; calyx 6–7 × 5 mm, margins intact, apically truncate with five prominent mucronate teeth, 0.5–1.0 mm long, the whole with minute raised glands; corolla funnelform-campanulate, exserted 45 mm above level of calyx lip, 3–4 mm wide at calyx mouth, 15–20 mm wide at mouth, glabrate with short hairs in region of ovary; corolla lobes 20–22 × 15–20 mm; stamens 15 or 22 mm long, shorter filaments inserted 1 mm and longer filaments inserted 5 mm above the level of the calyx lip, the staminode 5–6 mm long, inserted at the level of the calyx lip, anthers included; ovary 3 mm long, sparsely to densely lepidote, style 32 mm long, included. *Capsule* elongate-linear, 19–36 × 1.2–2.0 cm, many-seeded; seeds flattened, 1–2 × 3–4 cm, oblong with lateral membranous wings, each wing 1–1.5 cm long, margin subhyaline, 5–8 mm long, body ovoid, 2.0 × 1.2 cm, not conspicuously bipartite, not well differentiated from wings. Figure: Gentry (1977a: fig. 10).

Cydista decora is one of only two *Cydista* species restricted primarily or exclusively to South America, where it inhabits two disjunct regions: (1) western Ecuador, and (2) portions of Bolivia, Paraguay, and southwestern Brazil (Fig. 4). The two *C. decora* populations differ in that the Ecuadorian collections possess conspicuously though somewhat inconsistently bracteate inflorescences (Gentry, 1977b). The peak in flowering collections occurs in March and appears to be correlated positively with rainfall (Fig. 10), but collections of fruiting specimens are too few to determine fruiting phenology.

The generic affinity of *Cydista decora* was uncertain before fruiting material was known. Once fruiting material was available, Gentry (1977b) transferred it from the monotypic genus *Clytostomanthus* to *Cydista* and suggested that it may be closely related to *Cydista diversifolia,* although it differs, in part, by: (1) having larger flowers with a narrower calyx, (2) producing larger inflorescences, and (3) lacking glandular fields in the axils of the secondary veins beneath (although scattered, isolated glands are not uncommon). *Cydista decora* has more prominent calyx teeth than all other species in the genus.

Representative specimens. ECUADOR. **Chimborazo**: Río Chanchan, from Naranjapata to below Huigra, 02°16′S, 79°05′W, 2000–3000 m, *Camp E-3892* (F, US). **Esmeraldas**: W of San Mateo, Reserva Forestal de Jardín Tropical, 00°54′N, 79°37′W, 150 m, *Gentry & Lajones 73008* (MO). **Guayas**: Mocachi–Palenque, *Dodson et al. 14468* (MO[1]). **Los Ríos**: Jauneche, 01°30′S, 79°25′W, 100 m, *Dodson et al. 7507* (MO[1]). **Manabí:** vicinity of Agua Blanca, ca. 15 km of Puerto López, 01°28′S, 80°47′W, 590 m, *Hekker & Hekking 10259* (MO, QCA, U). BOLIVIA. **La Paz**: Alto Madidi, ridgetop ca 7 km NE of camp, 13°35′S, 68°46′W, 300 m, *Gentry & Estensoro 70713* (MO). **Santa Cruz**: San Juancito, 30 kms N de San Ignacio, 15°43′S, 67°16′W, 400 m, *Beck & Seidel 12407* (MO[1]). PARAGUAY. **Amambay**: P. N. Cerra Corsa, Pedro Juan Caballero, 22°39′S, 56°03′W, 300 m, *Solomon et al. 7015* (MO[1], PY). **Canindiyu**: 34 km E of Villa Ygatimi near Río Jejui-mi, 24°08′S, 55°32′W, 150 m, *Gentry et al. 59301* (MO). **San Pedro Chore**: proximidades de la Colonia Aquidaban Nigui, 3 km N de la Ruta, 24°00′S, 57°00′W, *Davalos 3* (MO[1]). BRAZIL. **Goiás**: Corumba, 15°55′S, 48°44′W, *Hoehne 5857* (R). **Mato Grosso do Sul**: Amambai, 3 km O Mato Grosso do Sul, 23°05′S, 55°13′W, *Hatschbach 45871* (MO[1]). **Minas Gerais**: Corumba, *Hoehne 5858* (MO[1]). **Paraná**: Porto São José, 22°43′S, 53°10′W, 246 m, *Hatschbach 5642* (MBM).

3. Cydista diversifolia (Kunth) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863. *Bignonia diversifolia* Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Quarto ed. 3: 133; Folio ed. 3: 104. 1819. *Pleonotoma diversifolium* (Kunth) Bureau & K. Schum., in Mart., Fl. Bras. 8: 274. 1897. TYPE: Mexico. Campeche: *Humboldt & Bonpland s.n.* (holotype, P).

Anemopaegma vargasianum DC., in A. DC., Prodr. 9: 190. 1845. *Cydista vargasiana* (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 192. 1863. TYPE: Venezuela. Caracas: *Vargas s.n.* (holotype?, G-DC).

Bignonia sagreana DC., in A. DC., Prodr. 9: 148. 1845. TYPE: Cuba. *Sagra s.n.* (holotype?, G-DC; isotype?, K).

Lianas, stems tetragonal, hollow in cross section, drying light to dark brown with four distinct and light-colored ridges, puberulent; pseudostipules foliaceous, to 1.0 × 1.5 cm, elliptic-orbicular, paired, entire. *Leaves* 8–12 cm long, once-pinnate with two primary, opposite leaflets and often a simple, terminal tendril; petioles 2–4 cm, sulcate, sparsely

lepidote, petiolules 1–3 cm, sulcate, sparsely lepidote; leaflets 5–8 × 4–7 cm, mostly ovate or ovate-elliptical, sometimes orbicular, apices acuminate to mucronate, bases truncate-rounded to slightly cordate, venation actinodromous (perfect, reticulate, basal) basally and brochidodromous apically, with 3–5 major veins, brown glandular fields often in axils of secondary veins, margins slightly undulate, chartaceous. *Inflorescences* to 20 cm long, several-flowered, peduncles 3.0–9.0 cm, the rachis and peduncles minutely bracteate, the bracts 1 mm long, pedicels 5 mm, sparsely lepidote-puberulent. *Flowers* ovoid in bud, apices straight; calyx 4–5 × 5–6 mm, generally drying uniformly dark, margin intact or shallowly split, apically truncate with five minute teeth; corolla funnelform-campanulate, exserted 35 mm past calyx lip, 4–5 mm wide at calyx mouth, 15 mm wide at mouth, glabrous except at fusion of filament and corolla tube where short, glandular hairs reside; corolla lobes 20–22 × 15 mm; stamens unequal, 13 or 16 mm long, inserted 1 mm below level of calyx lip, the staminode 6 mm long, inserted 1 mm below level of calyx lip, anthers included; ovary 3 mm long, lepidote, style 18 mm long. *Capsule* elongate-linear, 24–35 × 1.0–1.5 cm, reddish brown with inconspicuous longitudinal ridges, the central ridge most prominent, many seeded; seeds flattened, 1.0 × 3–4.5 cm, oblong with lateral membranous wings, each wing 1.2–1.8 cm long, body ovoid, 1.0 × 0.6 cm, clearly darker than wings, hyaline margin lacking.

Cydista diversifolia is a common liana, extending from the coastal regions of central Mexico to the Yucatán Peninsula and Cuba, and south through the Pacific side of Central America (Fig. 4). South American collections are restricted to central Colombia and northwestern and north-central Venezuela. Although it favors tropical dry forest, it may also occur in premontane moist and more infrequently tropical moist forests (Gentry, 1973b).

Gentry (1974) reported that *C. diversifolia* possesses a multiple-bang pollination syndrome and, like other species of *Cydista*, *C. diversifolia* apparently does not produce nectar and probably relies on deception of pollinators to effect pollen transfer. The number of flowering collections peaks in July or August (Fig. 11), and there are no significant phenological differences between Central and South American collections. Unlike other Mesoamerican *Cydista* species (*C. aequinoctialis*, *C. heterophylla*, and *C. potosina*), *C. diversifolia* initiates its peak flowering period after the onset of the wet season; flowering collections peak during the "vernillo" or lull of the wet season. Fruiting collections peak between November and January (Fig. 11).

Cydista diversifolia differs from other species of *Cydista* in its hollow branchlets, a character not previously reported for this species (perhaps because this character is readily detectable only in cleanly cut branchlets). Venation in *C. diversifolia* is nearly palmate, with the five principal veins joining at the base of the blade.

Representative specimens. MEXICO. **Campeche**: 28 km N de Escarcega, rumbo a Champoton, 18°37′N, 90°43′W, *Cabrera et al. 2045* (MO). **Chiapas**: Presa La Angostura, 45 km from Tuxtla, 16°34′N, 92°48′W, 700 m, *Breedlove 37440* (DS, MO[1]). **Guerrero**: El Pusulmiche, 3 km del Entronque de la Brecha a Corinto, Mun. Tecpan de Galeana, 17°15′N, 100°41′W, 60 m, *Tenorio et al. 1348* (MO[1]). **Jalisco**: La Huerta Est. de Invest., Exp. y Dif. Chamela, 19°32′N, 105°05′W, *Magallanes 3150* (MO[1]). **Michoacán**: 29 km al NE de Tumbiscatio, 18°31′N, 102°21′W, *Soto Núñez 3644* (MO[1]). **Oaxaca**: Cerro Arenal, Tehuantepec, 16°20′N, 95°14′W, 1000 m, *MacDougall s.n. (1971)* (F, MO[1]). **Quintana Roo**: 6 km N de Xel-Ha, 20°12′N, 87°20′W, *Téllez & Cabrera 3229* (MEXU, MO[1]). **Yucatán**: Chichén Itzá, 20°40′N, 88°34′W, *Gentry 537* (MO). GUATEMALA. **Chiquimula**: between Chiquimula and La Laguna, 14°48′N, 89°33′W, 500–1000 m, *Steyermark 30680* (F). **Izabal**: 25 km W of El Estor, 15°32′N, 89°21′W, *Harmon & Dwyer 4319* (MO[1]). **Petén**: along road on N shore of Lake Petén, 16°59′N, 89°50′W, *Croat 24725* (MO[1]). BELIZE. **Belize**: W of Benque Viejo near border with Guatemala, 17°06′N, 89°08′W, *Gentry 8264* (F, MO[1]). **Cayo**: Xuanantunich, Maya ruins just NW of Benque Viejo, 17°05′N, 89°08′W, *Ugent 13* (MO, WIS). **Toledo**: 2–4 mi. W of San José Rd., 16°26′N, 89°02′W, 200–366 m, *Gentry 8188* (MO[1]). HONDURAS. **Choluteca**: vic. of Choluteca, 13°18′N, 87°12′W, 20 m, *Standley 24406* (F). **Comayagua**: Los Manjas Station, 7 km N of Comayagua, 14°25′N, 87°37′W, 600 m, *D'Arcy 18146* (MO). **Copán**: 4 mi. E of Copán, 14°50′N, 89°09′W, 800 m, *Croat 42501* (MO). **Cortés**: Quebrada El Encanto, Montana la Cumbre, 15°30′N, 88°00′W, 200 m, *Molina 3594* (F). **Morazán**: Río de la Orillo, 14°30′N, 87°00′W, *Rodríguez 817* (F). **El Paraíso**: 15 km S of El Paraíso, 14°10′N, 86°30′W, 1300 m, *Molina 18422* (F). **Valle**: Puerto de San Lorenzo, 13°30′N, 87°35′W, 0 m, *Molina 5396* (F). **Yoro**: vic. of Coyoles, near Medina, 15°15′N, 87°15′W, 200 m, *Yuncker et al. 8623* (F). EL SALVADOR. **La Libertad**: 6 mi. NW of La Libertad, 13°29′N, 89°19′W, *Wunderlin et al. 743* (MO). NICARAGUA. **Boaco**: 4 km al S de Boaquito, San Antonio, 12°26′N, 85°44′W, 200 m, *Moreno 18011* (MO[1]). **Carazo**: between Amayito and Barranco Bayo, 11°40′N, 86°18′W, 30–100 m, *Stevens 22764B* (MO[1]). **Chontales**: Hda. Corpus W of Juigalpa, 12°07′N, 85°28′W, 100 m, *Stevens 21785* (MO). **Estelí**: Mechapa, 3 km al N de la Trinidad sobre la carretera Panamericana, 12°59′N, 86°14′W, 700 m, *Moreno 22436* (MO[1]). **Granada**: Casa Tejas, 11°46′N, 85°54′W, 40 m, *Moreno 17091* (MO). **León**: El Velero, at mouth of Estero San José, ca. 10 km by road S of Hwy. 32, 12°08′N, 86°45′W, 3 m, *Stevens 23050* (MO[1]). **Managua**: Carretera Panamericana, 12°21′N, 86°03′W, 90–100 m, *Moreno 1215* (MO[1]). **Masaya**: Laguna de Apoyo, 11°56′N, 86°04′W, 100 m, *Moreno 3932* (MO[1]). **Matagalpa**: Las Playitas de Moyua NE de Lago Moyua, 12°37′N, 86°04′W,

475 m, *Sandino & Guzmán 844* (MO!). **Rivas**: El Coyol Tola–Las Salinas, 11°23′N, 85°58′W, 35 m, *Stevens 9745* (MO!). COSTA RICA. **Alajuela**: Llanos de Turrúcares, 09°54′N, 83°33′W, *Pittier 16436* (CR, US). **Guanacaste**: Paloverde, OTS Field Station, 8 km W of Bagaces, 10°32′N, 85°18′W, 100 m, *Gentry et al. 71450* (MO). **Limón**: La Bomba–Cahuita, 09°44′N, 82°50′W, 20 m, *Gómez & Hampshire 20130* (MO). **Puntarenas**: Isla del Caño, 17 km NW of Pta. Llorona, 08°37′N, 83°44′W, *Janzen 11641* (MO). **San José**: La Garita–Alajuela en propiedad del ICE, 09°59′N, 84°20′W, *Poneda & FcoCiccia 4172* (WIS). PANAMA. **Canal Zone**: Boy Scout Camp road near Madden Lake, 09°15′N, 79°35′W, *Gentry 2480* (MO). **Colón**: Quebrada Ancha, 3 km N of Clement Plant, 4 km ENE of Buena Vista, 100 m, *Nee 9122* (MO!). **Panamá**: Madden Lake, 09°15′N, 79°35′W, *Gentry 5012* (MO).

CUBA. Cienfuegos Central Soledad, 22°09′N, 80°27′W, *Howard 4785* (B, C, CLEMS, L, TEX-LL, MEXU, MI). **La Habana**: Sierra de Anafe, 22°55′N, 82°40′W, 200 m, *Gentry & Hammel 71228* (MO). **Las Villas**: Loma de Bauao, 20°28′N, 76°22′W, *León & Luna 21956* (HAC). **Matanzas**: Playa on road from Buryvaea, 23°02′N, 81°34′W, *Britton et al. 556* (CM). **Oriente**: Sabanaso, 20°48′N, 76°42′W, *Ekman 7433* (AAU, B). **Pinar del Río**: Sierra de Anafe, *Ekman 13029* (B, MO).

COLOMBIA. **Antioquia**: Currulao Nueva Antioquia, 11 km E-NE de Turbo, 08°06′N, 76°43′W, 45 m, *Callejas et al. 5011* (COL, MO!). **Atlántico**: Usiacuri, camino de Isabel López, 10°45′N, 74°59′W, 100 m, *Dugand & García-Barriga 2323* (COL). **Bolívar**: Mun. Cartagena, Isla de Tierrabomba, 10°20′N, 75°32′W, 5–30 m, *Cuadros 4338* (MO!). **Cesar**: Gamara, Pto. Nacional, 10°22′N, 73°08′W, 70 m, *Uribe-Uribe 2409* (COL). **Cundinamarca**: 14 km S of Melgar, 04°12′N, 74°39′W, 400 m, *Gentry et al. 8972* (COL, MO). **Guajira**: Maicao, near El Ocho, 11°23′N, 72°13′W, *Bunch 212* (MO!). **Huila**: 17.5 km N of Neiva, 03°02′N, 75°19′W, 640 m, *Croat 55260* (MO!). **Magdalena**: Fundación, Santa Rosa, 09°25′N, 74°05′W, 200 m, *Romero-Castañeda 11055* (MO!). **Norte de Santander**: Río Peralonso, alrededores de Santiago, 07°52′N, 72°43′W, 120 m, *Araque & Barkley 18NS104* (COL). **Santander**: 17 km NE of Socorro toward San Gil, 06°29′N, 73°16′W, 1250 m, *Gentry & Forero 15338* (MO!). **Sucre**: Corozal, Palmitos, 09°19′N, 75°18′W, *Romero-Castañeda 9356* (COL). **Tolima**: Flandes, Finca San Rafael, 04′18′N, 74°49′W, 350 m, *Escobar et al. 158* (MED). **Valle**: Cali, 03°27′N, 76°31′W, 900 m, *Forero & Hernández 1555* (MO). VENEZUELA. **Aragua**: Tejeria–La Encrucijada, 10°15′N, 67°10′W, *Aristeguieta 4311* (MO!, VEN). **Carabobo**: Carretera de Maracay a Valencia, 10°05′N, 68°05′W, 400 m, *Williams 12193* (VEN). **Cojedes**: Via hacia Tinaco, cerca puente los Monos, 09°42′N, 68°26′W, 150 m, *Rojas 475* (MV). **Distrito Federal**: behind Univ. Católica Andrés Bello, Montalbán, Caracas, 10°30′N, 66°55′W, *Berry 1283* (MO!). **Falcón**: Sierra de San Luis, carretera Coro–La Tabla, 11°07′N, 69°42′W, 600 m, *Flora Falcón 818* (MO!). **Guárico**: 19 km N of Altagracia de Orituco, 08°21′N, 67°24′W, 500 m, *Gentry & Berry 15116* (MO!). **Lara**: El Placer, cerca de Cabudare, 10°02′N, 69°16′W, 443 m, *Saer 621* (F, M, VEN). **Miranda**: Carretera Carenero–Chirimena, 2 km NW of Carenero, 10°32′N, 66°07′W, 0–5 m, *Steyermark & Bunting 102300* (NY, VEN). **Portuguesa**: 20 km al SO de Guanare, 09°03′N, 69°45′W, 200 m, *Aymard & Ortega 2844* (MO!). **Táchira**: Matorrales, 07°52′N, 72°19′W, 1000 m, *Bono 5044* (MO!). **Trujillo**: El Cenizo, 09°25′N, 70°30′W, 30 m, *Lasser 2832* (VEN). **Yaracuy**: Hacienda Iboa, near Guama, 10°20′N, 68°45′W, *Pittier 11158* (VEN US). **Zulia**: Dtto. Mara, Guasare–Socuy, 10°52′N, 72°29′W, 100 m, *Bunting 10319* (MO!).

4. Cydista heterophylla Seibert, Publ. Carnegie Inst. Wash. 522: 417. 1940. TYPE: Mexico. Yucatán: *Lundell & Lundell 7350* (holotype, MICH; isotypes, A, F, US).

Bignonia lepidota Seem., Bot. Voy. Herald 179. 1854, non Kunth. TYPE: Panama. Isla de Iguana: *Cuming 1262* (isotype?, K).

Lianas, stems terete, solid in cross section, drying gray to brownish, inconspicuously lenticellate, glabrous; pseudostipules inconspicuous. *Leaves* 11–17 cm long, once-pinnate with two primary, opposite leaflets and often a simple, terminal tendril; petioles 2–3 cm, sulcate, sparsely puberulent, petiolules 2–3 cm, sulcate, sparsely puberulent; leaflets 7–12 × 4–7.5 cm, ovate to ovate-elliptic, apices acuminate to acute, bases obtuse or rounded, venation actinodromous basally (three principal veins conjoining) and brochidodromous apically, 3–4 vein pairs, glandular fields in axils of secondary veins inconspicuous and infrequent, margins slightly undulate, chartaceous. *Inflorescences* to 14 cm long, several- to many-flowered, peduncles 0.3–1.0 cm, the rachis and peduncles minutely bracteate, bracts 1 mm or less, pedicels 11 mm, lepidote. *Flowers* ovoid in bud, apices straight; calyx 4–5 × 4–5 mm, generally drying uniformly dark, margin shallowly split, sometimes appearing bilabiate, teeth lacking, densely lepidote; corolla funnelform-campanulate, exserted 40 mm above level of calyx lip, 2–3 mm wide at calyx mouth, 15 mm wide at mouth, glabrous; corolla lobes 15 × 15 mm; stamens unequal, 11 or 16 mm long, inserted 5 mm above level of calyx lip, the staminode 3 mm long, inserted 4 mm above level of calyx lip, anthers included; ovary 3 mm long, lepidote, style 28 mm long, included. *Capsule* elongate-linear, 20–35 × 1.7–2.0 cm, brown with minute dark glands and two conspicuous darkened submarginal ridges, many seeded; seeds 1.5 × 7 cm, oblong with lateral membranous wings, 3.0–3.5 cm long, becoming hyaline 5–8 mm from margin, body ovoid, not well differentiated from wings, not obviously bipartite but the dark midline extending ⅓ length of body. Figures: Gentry (1973b: fig. 10, p. 841), Gentry (1982: fig. 10, p. 101).

Cydista heterophylla is a common liana of tropical dry forests and drier areas of moist forests, occurring less commonly in moist regions (Gentry, 1973b). Its range extends from central Mexico to

the Yucatán Peninsula, south through Central America, and to the extreme northwestern portions of Colombia (Fig. 5).

Flowering is initiated prior to the onset of the wet season, and flowering collections peak in May, after which numbers of flowering collections decrease markedly (Fig. 12). Fruiting collections peak slightly from November to February (Fig. 12).

Seibert (1940) distinguished *Cydista heterophylla* by its conspicuously bilabiate calyces and production of flowers during the dry season while essentially leafless. Gentry (1973b) reported that *C. heterophylla* has "a propensity to simple leaves," and that the leaflets possess "a basal pair of arcuate veins with glandular fields in their axils." Many plants, especially juveniles, often exhibit two terminal pairs of simple leaves that mimic a whorl of four (Gentry, 1973b).

Representative specimens. MEXICO. **Campeche**: El Tormento, 5 km W of Escarcega, 18°37′N, 90°43′W, *Held et al. FC86* (U). **Chiapas**: 5.6 mi. E of Chiapa de Corzo, 16°42′N, 93°00′W, 833 m, *Breedlove 9559* (DS, F, MEXU). **Guerrero**: Zihuatenejo, rumbo a Isetla, 17°38′N, 101°33′W, *German et al. 269* (MEXU). **Jalisco**: Puerto Vallarta, 20°37′N, 105°15′W, 16 m, *Croat 45406* (MO[1]). **Nayarit**: 6 mi. E of San Blas, 22°52′N, 105°06′W, *Johnson 242-73* (MO). **Oaxaca**: Mun. Matías Romero, 8 km S de Esmeralda, 17°06′N, 94°48′W, 150 m, *Wendt et al. 4809* (MO[1]). **Quintana Roo**: En los alrederores de el Ramoral, 18°25′N, 88°30′W, *Ramamoorthy et al. 2130* (MO[1]). **Tabasco**: 10–40 km W of Huimanguillo, 17°51′N, 93°23′W, *Barlow 30/161* (MEXU, MICH, WIS). **Veracruz**: Banos de Carrizal, 5 km SE of Emiliano Zapata, 19°20′N, 96°37′W, 220 m, *Nee & Taylor 26601* (MO[1]). **Yucatán**: near Xocenpich, 20°46′N, 88°35′W, *Lundell & Lundell 7350* (A, F, TEX-LL, MICH, US). GUATEMALA. **Petén**: Santa Elena, Poctun, 16°06′N, 90°27′W, *Tun 1189* (F, MO[1]). BELIZE. **Cayo**: 4.5 km before Caracol, 16°46′N, 89°07′W, *Balick et al. 3152* (MO[1]). **Orange Walk**: Indian Church, 17°45′N, 88°40′W, *Arnason & Lambert 17341* (MO[1]). **Stann Creek**: Stann Creek Railway, 16°58′N, 88°13′W, 33 m, *Schipp 224* (F, MICH, MO[1]). **Toledo**: 2–4 mi. W of San José road, 16°15′N, 89°02′W, 200–366 m, *Gentry 8192* (MO[1]). HONDURAS. **Choluteca**: 5 km NW of San Francisco, 13°33′N, 87°16′W, *Lent 598* (MO[1]). **Comayagua**: La Cana, San Louis, 14°25′N, 87°37′W, 833 m, *Edwards P-597* (F, MICH). **Copán**: Entre San Nicolás y Trinidad, carretera Santa Rosa de Copán, 14°57′N, 88°45′W, 100 m, *Molina 11725* (F). **Cortés**: Entre Cofradia y Montana Cusuco, 15°30′N, 88°00′W, 1000 m, *Molina 7302*, (F). **Morazán**: Zamorano, 14°30′N, 87°00′W 850 m, *Molina 115* (F). **Yoro**: Entre Yoro y Morazán, 15°15′N, 87°15′W, 700 m, *Molina 6925* (F). EL SALVADOR. **La Unión**: Carretera a La Laguna de Olomega, 13°19′N, 88°04′W, *Lagos 625* (MO[1]). NICARAGUA. **Chinandega**: Camino de Puerto Morazán a Tonala, 12°50′N, 87°09′W, 30–40 m, *Sandino & Martínez 4363* (MO[1]). **Chontales**: Camino entre Juigalpa y Puerto Díaz, 12°05′N, 85°24′W, 31–130 m, *Guzmán et al. 373* (MO[1]). **Estelí**: Mechapa, 3 km al N de La Trinidad sobre la carretera Panamericana, 12°59′N, 86°14′W, 700 m, *Moreno 22435* (MO[1]). **Granada**: Casa Tejas, 11°46′N, 85°54′W, 40 m, *Moreno 17090* (MO[1]). **León**: Quebrada of Las Ruedas, NW of El Tránsito, 12°05′N, 86°43′W, 15–30 m, *Stevens et al. 20138* (MO[1]). **Managua**: Carretera a Montelimar, 11°49′N, 86°31′W, 10 m, *Guzmán et al. 438* (MO[1]). **Masaya**: P. N. Volcán Masaya, 11°59′N, 86°10′W, 300 m, *Neill 3135D* (MO[1]). **Matagalpa**. Puertas Viejas, 1–2 km camino a San José de los Remates, 12°35′N, 86°01′W, 430–470 m, *Moreno 16263* (MO[1]). **Nueva Segovia**: El Jícaro, Casa Viejas, 13°44′N, 86°05′W, 600 m, *Moreno 13505* (MO[1]). **Rivas**: Isla Ometepe, Volcán Maderas, Mérida, 11°27′N, 85°33′W, 240 m, *Robleto 397B* (MO[1]). **Zelaya**: Kurinwacito, 13°08′N, 84°55′W, *Moreno 23975* (MO[1]). COSTA RICA. **Alajuela**: between Caldera and Orotina near Sitio Huacas, 09°54′N, 83°33′W, 150 m, *Gentry et al. 71439* (MO[1]). **Guanacaste**: Parq. Nac. Santa Rosa road to Estero Real, 10°50′N, 85°35′W, 150 m, *Hufi et al. 2103* (MO). **Puntarenas**: Barranca forest, vicinity of Miramar turnoff, 10°06′N, 84°44′W, *Gentry 1332* (MO). PANAMA. **Canal Zone**: Barro Colorado Island, 09.11N, 79.57W, *Croat 8206* (MO[1], SCZ). **Darién**: El Real, 08°08′N, 77°43′W, *Gentry 4575* (MO[1]). **Herrera**: 12.5 mi. E of Las Minas, 07°48′N, 80°44′W, *Gentry 3143* (MO). **Panamá**: Río Espavé, 09°14′N, 78°46′W, *Gentry 3700* (MO[1]).

CUBA. **La Habana**: 23°08′N, 82°22′W, *Sagra 89* (MO, F).

COLOMBIA. **Bolívar**: Mun. Turbaco, La Cantera de Cimaco, near Cartagena, 10°20′N, 75°25′W, 100 m, *Gentry et al. 78483* (MO[1]). **Sucre**: Estación de Primatos, 09°30′N, 75°30′W, 300 m, *Gentry & Cuadros 68146* (MO).

5. Cydista lilacina A. H. Gentry, Mem. New York Bot. Gard. 29: 277. 1978. TYPE: Venezuela. Bolívar: *Gentry, Morillo & de Morillo 10673* (holotype, MO[1]; isotypes, MO[1], VEN).

Lianas, stems terete, solid in cross section, generally drying dark brownish green to dark gray, glabrous; pseudostipules inconspicuous. *Leaves* 20–25 cm long, once-pinnate with two primary, opposite leaflets and frequently a simple, terminal tendril; petioles 2.5–6 cm, inconspicuously sulcate, lepidote, petiolules 1.5–4 cm, conspicuously sulcate, lepidote; leaflets 11–19 × 5–14 cm, mostly broadly ovate-elliptical, occasionally ovate, apices obtuse-mucronate to acuminate, bases obtuse or rounded, occasionally oblique, venation actinodromous basally and brochidodromous apically, 4–5 vein pairs, midrib and secondaries prominent abaxially with dark confluent or isolated glands in axils of secondary veins, occasional dark glands throughout blade, margins slightly undulate, chartaceous. *Inflorescences* to 19 cm long, several-flowered, peduncles 6.0–11.5 cm, the rachis and peduncles minutely bracteate, pedicels 5 mm, lepidote. *Flowers* ovoid in bud, apices curved; calyx 6–7 × 4.5 mm, drying uniformly dark, margin shallowly split, teeth five and minute, lepidote, ciliate with uniseriate hairs; corolla exserted 40 mm above level of calyx lip, 2–3 mm wide at calyx tip, 15 mm wide at mouth, stalked glandular hairs overall; corolla lobes

20–22 × 15 mm, irregularly elliptic; stamens unequal, 13 or 20 mm long, inserted 1 mm below level of calyx lip, the staminode 5 mm long, inserted 1 mm below level of calyx lip, anthers included; style 25 mm long, included; ovary 3 mm long, lepidote, ovules 4-seriate. *Capsule* elongate, 16–32 × 3–4 cm, surface wrinkled, many-seeded; seeds flattened, 1–2 × 4–5 cm, elliptic-oblong with lateral membranous wings, each 1.5–2.0 cm long, hyaline margin 3–5 mm, body ovoid, not clearly distinct from wings, bipartite with distinct longitudinal ridge. Figure: Gentry (1978: fig. 125).

Cydista lilacina is one of two almost exclusively South American *Cydista* species; a single collection from Costa Rica is known (Fig. 6). Collections are infrequent and distributed throughout South America north of Paraguay. *Cydista lilacina* is relatively common in only two regions: (1) northern Bolivia, eastern Peru, and western Brazil, and (2) eastern Venezuela. Flowering collections are few and appear to peak in October (Fig. 13). If this peak represents the true peak in flowering for the species, *C. lilacina* would be the latest-flowering species of the genus (precipitation was not plotted with phenology data because the paucity of and wide distribution of fertile collections precludes comparisons to any localized region).

Cydista lilacina differs from all other *Cydista* species in its 4-seriate ovules and curved bud apices. Capsules of *C. lilacina* and *C. potosina* are generally wider than those of all other species. However, the wrinkled surface of *Cydista lilacina* capsules differs from the smooth surface typical of capsules of *C. potosina* (Gentry, 1978). Vegetatively, *C. lilacina* resembles wide-leaved specimens of *C. aequinoctialis* but possesses round rather than subtetragonal branchlets.

Representative specimens. COSTA RICA. **Puntarenas**: Reserva Biologica Carara, 09°46′N, 84°29′W, 20 m, *Zúñiga 90* (CR, MO).

COLOMBIA. **Bolívar**: Santuario Nacional de Los Colorados, Mun. San Juan Nepomuceno, 09°58′N, 75°10′W, 230–250 m, *Gentry et al. 60654* (JBGP, MO). ECUADOR. **Pastaza**: 2 km del pueblo de Villano, 01°25′S, 77°20′W, 400 m, *Tipaz et al. 485* (MO[1]). PERU. **Huánuco**: carretera Marginal, S of Bosque von Humboldt, 08°45′S, 75°01′W, 270 m, *Gentry & Jaramillo 41326* (MO). **Junín**: entre Santa Ana y Pampatigre, 11°50′S, 75°50′W, 900 m, *Fernández et al. 151* (MO[1], USM). **Loreto**: Dtto. Calleria Bosque Nac. Alex. Humboldt, 250–300 m, *Schunke 10396* (AAU, MO[1]). **San Martín**: 07°11′S, 76°33′W, 350 m, *Gentry & Smith 44983* (MO[1]). **Ucayali**: Bosque von Humboldt, 08°40′S, 75°00′W, 250 m, *Gentry et al. 29527* (MO[1]). BOLIVIA. **La Paz**: Alto Madidi across from mouth of Río Enlatagua, 13°35′S, 68°46′W, 280 m, *Gentry & Estensoro 70274* (MO). **Pando**: Carretera entre San Silvestre y Cu Curichon, 11°51′S, 68°37′W, *Beck et al. 19589* (MO[1]). SURINAME. **Nickerie**: Kabalebo Dam area, 03°34′N, 55°59′W, 30–130 m, *Lindeman & Roon 741* (MO[1]). VENEZUELA. **Amazonas**: Dept. Atures, San Juan de Manapiare, 05°18′N, 66°03′W, 150 m, *Huber 1056* (MO[1]). **Barinas**: Carretera La Yuca–Barinitas, 08°45′N, 70°25′W, *Marcano-Berti et al. 112-980* (IPA, MBM, MO[1], U). **Bolívar**: 2–15 km E of La Paragua–Ciudad Piar hwy., on road to San Pedro, 06°50′N, 63°20′W, 300 m, *Gentry & Berry 15063* (MO[1]). **Delta Amacuro**: E of El Palmar, 08°20′N, 61°40′W, *Gentry & Berry 14987a* (MO[1]). **Sucre**: Pen. Paria, between Guacoco and Guaratarо, 10°43′N, 62°48′W, 80 m, *Steyermark & Liesner 121011* (MO[1]). BRAZIL. **Acre**: on Río Branco Santa Rosa, 08°14′S, 73°13′W, *Lowrie et al. 440* (MO[1]). **Amazonas**: basin of Río Jurua, near mouth of Río Embira, 07°30′S, 70°15′W, *Krukoff 5046* (MICH, MO[1], US). **Maranhao**: St. Luzia, Reserva Florestal de Buriticupu, 03°08′S, 42°54′W, *dos Santos et al. 70* (MO[1]). **Mato Grosso**: Barra do Bugres, entre Denise e Arenapolis, 15°05′S, 57°11′W, *Saddi 4323* (CH). **Minas Gerais**: W side of Río Aripuana, below Salto dos Dardanelos, 20°41′S, 46°15′W, *Berg et al. P18531* (CH, MO). **Pará**: Parauapebas, Reserva Biologica da Serra dos Carajas, 07°45′S, 51°30′W, 600 m, *dos Santos et al. 218* (MO[1]). **Rondônia**: Río Jaru, estrada Porto Velho–Cuiaba, 10°05′S, 61°59′W, *Duarte & Appa 7038* (MO[1], RB, INPA). **Roraima**: SEMA Ecological Station, Ilha de Maraca, 03°22′N, 61°25′W, *Ratter et al. R5373* (MO[1]).

6. Cydista potosina (K. Schum. & Loes.) Loes., Repert. Spec. Nov. Regni Veg. 16: 209. 1919. *Arrabidaea potosina* K. Schum & Loes., Bull. Herb. Boissier 3: 618. 1895. TYPE: Mexico. San Luis Potosí: *Seler 616* (holotype, B not seen by Gentry).

Clytostoma mayanum Standl., Carnegie Inst. Wash. Publ. 461: 86–87. 1935. TYPE: Guatemala. Petén: Yaxha–Remate Road, *Lundell 4008* (holotype, F; isotype, S).

Lianas, stems tetragonal, solid in cross section, drying gray with four distinct and often light-colored ridges, glabrous; pseudostipules linear-triangular, numerous, overlapping, usually less than 8 mm long. *Leaves* 6–14 cm long, once-pinnate with two primary, opposite leaflets and often a simple, terminal tendril; petioles 1–4 cm, inconspicuously sulcate, puberulent, petiolules 1–4 cm, sulcate, puberulent; leaflets 4–10 × 2–5 cm, mostly ovate to ovate-elliptical, apices acuminate, bases rounded to obtuse, venation brochidodromous, 4–5 vein pairs, veins puberulent-pilose beneath, solitary glands in axils of secondary veins occasionally present, margins slightly undulate, chartaceous. *Inflorescences* to 10 cm long, ca. 4–8-flowered, peduncles 0.5–8.5 cm, the rachis and peduncles minutely bracteate, pedicels ca. 5 mm, lepidote. *Flowers* ovoid in bud, apices straight; calyx 2–7 × 5–6 mm, apically truncate with five minute teeth, drying dark basally and lighter apically, lepidote with dense aggregations of hair; corolla funnelform-campanulate, exserted ca.

35 mm above level of calyx lip, 2–3 mm wide at calyx mouth, ca. 15 mm wide at mouth, lepidote; corolla lobes 16 × 20 mm, irregularly elliptical; stamens 5, unequal, 10 or 17 mm long, filaments paired, distinct, adnate to corolla tube, shorter filaments inserted 2 mm and longer ones 5 mm above level of calyx lip, the staminode 3 mm long, inserted at level of calyx lip, anthers with two spreading thecae, subterminal on the filament; disk wanting, ovary 3 mm long, cylindrical, lepidote, style ca. 30 mm long, included, stigma bipartite, divisions laterally flattened. *Capsule* elongate, 20–24 × 2.8–3.2 cm, drying dark, surface smooth, many-seeded; seeds flattened, 1.5 × 6 cm, oblong with lateral membranous wings, each 1–2 cm wide, frequently unequal, margin hyaline, 1 mm or less, body ovoid, not obviously bipartite but with dark medial ridge extending ½ length of seed.

Cydista potosina (Fig. 1) has the most restricted distribution of all *Cydista* species (Fig. 6); it ranges from the southeastern half of central Mexico to the Yucatán Peninsula and Belize, with sporadic collections from Guatemala, Honduras, El Salvador, and Nicaragua. A single collection is known from Costa Rica. Gentry (1982) reported a "multiple-bang" flowering phenology in *C. potosina*. Flowering collections peak in June and decline sharply by August (Fig. 14). Like *C. aequinoctialis* and *C. heterophylla*, *C. potosina* appears to initiate flowering before the onset of the wet season. Fruiting collections are evenly distributed from September to March (Fig. 14).

Cydista potosina differs from all other *Cydista* species in its distinctive, bicolorous (when dried), ciliate-margined calyx. *Cydista potosina* and *C. lilacina* have capsules that are wider than those of other *Cydista* species. The branchlets of *C. potosina* and *C. decora* are tetragonal and frequently dark with four light-colored, longitudinal ridges. The leaflet venation of *C. potosina* more closely resembles the uniformly brochidodromous type of *Clytostoma*, rather than the basally actinodromous type of many *Cydista* species. The pseudostipules of *C. potosina* are reminiscent of the bromeliad-type clusters typical of *Clytostoma*, which further suggests a relationship between the two genera. However, the smooth, lepidote ovary and smooth fruit of *C. potosina* indicate a closer affinity to *Cydista* than to *Clytostoma*.

Representative specimens. MEXICO. **Campeche**: Hopelchen, 10 km de Xpujil, 18°12′N, 89°26′W, *Chan 1289* (XAL-M). **Chiapas**: Chicomuselo, 15°46′N, 92°16′W, 650 m, *Matuda 5652* (MEXU, TEX-LL). **Oaxaca**: Mun. M. Romero, 7.2 km O de Esmeralda, 17°08′N, 94°50′W, 100 m, *Wendt et al. 3618* (MO[1]). **Puebla**: M. Sn. Diego, 18°50′N, 98°00′W, *Ramírez 258* (MEXU). **Quintana Roo**: 1 km NW of Puerto Morelos, 20°50′N, 86°52′W, 5 m, *Davidse et al. 20022* (MO[1]). **San Luis Potosí**: San Antonio, La Ladrillera, 22°08′N, 100°59′W, 300 m, *Alcorn 3199* (MO[1]). **Tabasco**: Cerro las Campanas, 3 km E of Teapa, 50 km S of Villahermosa, 17°33′N, 92°57′W, 50–100 m, *Conrad & Conrad 2813* (MO[2], MEXU). **Veracruz**: Cerro El Vigía Estación de Biología Tropical Los Tuxtlas, 450 m, *Sinaca-Colin 144* (MO). **Yucatán**: Chamul, village 8 km from Xuilub, 25m, *Mogensen 1038* (MO[1]). GUATEMALA. **Escuintla**: slopes of the Río Coyolate, 13°57′N, 91°19′W, *Harmon 2379* (MO[1]). **Izabal**: across bay from Puerto Barrios, 15°43′N, 88°36′W, 20–50 m, *Steyermark 39853* (F). **Petén**: Remate, 13 km NE of Village, 17°00′N, 89°42′W, *Contreras 927* (MO[1], TEX-LL). BELIZE. **Belize**: W of Spanish Lookout, road to ferry, 17°13′N, 88°59′W, *Dwyer et al. 461* (MO). **Cayo**: near Teakettle, 17°14′N, 88°51′W, *Whitefoord 3317* (MO[1]). **Corozal**: 18°24′N, 88°24′W, *Gentle 181* (MICH). **Stann Creek**: Cockscomb Mts, 16°48′N, 88°37′W, 100–166 m, *Gentry 8001* (MO[1]). **Toledo**: Southern Hwy., 14 mi. N of Punta Gorda–San Antonio, 16°15′N, 89°02′W, 100–166 m, *Gentry 8228* (F, MO[1]). HONDURAS. **Atlántida**: E of Tela near Yoro Trail, 15°44′N, 87°27′W, *Yuncker 4973* (F, MICH, MO[1]). **Yoro**: near the village of Los Flores, 15°15′N, 87°15′W, 950 ft., *Yuncker et al. 8163* (MO[1]). NICARAGUA. **Chontales**: 2.6 km NW of Cuapa, 12°16′N, 85°23′W, 500 m, *Stevens & Montiel 17441* (MO). **Jinotega**: 21 km del Valle del Cua, NW de El Cedro, 13°30′N, 85°38′W, 700 m, *Moreno 944* (MO[1]). **Nueva Segovia**: Río Diplito, E de Ciudad Ocotal, 13°37′N, 86°27′W, *Sandino 2995* (MO[1]). COSTA RICA. **Puntarenas**: Parque Nacional Corcovado, Pavo Forest, 08°27′N, 83°33′W, 0–150 m, *Kernan 573* (CR). EL SALVADOR. **Ahuachapán**: El Imposible, cerca de los Enganches, 13°52′N, 89°59′W, *Sermeno 175* (MO[1]). **La Libertad**: Hacienda La Argentina, 13°40′N, 89°20′W, 500 m, *Montalvo 4267* (ITIC).

Dubious or Rejected Names

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Index to Exsiccatae

Collections are listed alphabetically by the principal author, followed by collection number, and a boldface number (**1–6**) designating the species collected. All specimens entered into TROPICOS were assumed to have been examined by A. H. Gentry. Specimens examined by the author were limited to duplicates housed at MO, and are indicated by a "!" in superscript. Collections cited under "representative specimens" are not included in the Index to Exsiccatae. The coding of the species numbers is as follows: **1a** = *Cydista aequinoctialis* var. *aequinoctialis*, **1b** = *Cydista aequinoctialis* var. *hirtella*, **2** = *Cydista decora*, **3** = *Cydista diversifolia*, **4** = *Cydista heterophylla*, **5** = *Cydista lilacina*, and **6** = *Cydista potosina*.

Abbott 1446 **1a**; *Acevedo 2810*! **1a**, *3318*! **1a**, *3443*! **1a**; *Acuna et al. 24151* **3**; *Agostini & Agostini 1052* **1a**; *Aguilar 259*! **4**, *40* **6**, *s.n.* **3**; *Alain 1417* **3**; *Alcorn 2172*! **6**; *Allen 127*! **1a**, *173* **1a**, *3250* **1a**, *1756*! **4**, *1964*! **1a**, *2458* **1a**, *2503* **1a**, *2641* **1a**, *3646* **1a**, *6520* **1a**, 6589 **3**, *858*! **1a**; *Almeda et al. 3115* **3**; *Alston 5609* **1a**, *8815* **1**, *8865* **4**, *8865A* **1a**; *Alvarez et al. 812*! **1a**; *Amaral et al. 341*! **1a**; *Americo 12671*! **1a**; *Ansouin 621* **3**; *Antonio 4241*! **1a**; *Apolinar 383* **3**; *Araquistain 110*! **3**, *261*! **3**, *2973*! **3**, *306*! **3**; *Araquistain & Moreno 530*! **3**; *Archer 8333* **1a**; *Aristeguieta 2259* **1a**, *4312* **3**, *4313*! **3**, *5154*! **1a**, *6438*! **3**; *Arnason 17739*! **3**; *Arnason & Lambert 17710*! **3**; *Arturo & Magallanes 3150* **3**, *3563* **1a**, *828* **3**; *Arvigo 133*! **3**; *Arvigo et al. 557* **4**; *Atwood & Neill AN207*! **3**; *Aubréville 364* **1a**, *40*! **1a**; *Austin 4173*! **1a**; *Austin et al. 7013* **1a**, *7326*! **1a**; *Aviles X-1*! **1a**, *X-8*! **1a**; *Axelrod 2001*! **1a**, *2438*! **1a**; *Ayala 2376*! **1a**, *2504*! **1a**, *3717* **1a**; *Aymard 3395*! **1a**; *Aymard & Delgado 8454*! **1a**; *Aymard & Ortega 2844*! **3**; *Aymard et al. 10212*! **5**, *370*! **1a**, *3942*! **1a**.

Bach s.n. MG4157 **1a**; *Bachbett s.n.* **6**; *Badillo 2024* MV **1a**; *Bailey 227* **3**; *Bailey & Bailey 132* **1a**, *610* **1a**; *Balee 1981* **5**, *2596* **5**; *Balick et al 3153* **6**, *1488*! **1a**, *3152*! **4**; *Balsev 97298* **1a**; *Balsev et al. 97298* **1a**; *Bangham 422* **1a**, *605* **1a**; *Barbier s.n.*! **1a**; *Barclay s.n.* **1a**; *Barkley et al. 17M755* **3**; *Barlow 32/18* **6**, *32118A* **6**; *Barr & Mason 62-327* **1a**; *Barrier 4027*! **1a**; *Bartlett 12439pp* **6**; *Stergios & Delgado 12893* **1a**; *von Bayern 332* M **1a**; *Beck 3798*! **1a**; *Beck et al. 20381*! **5**; *Benítez de Rojas 475*! **3**, *1127* **1a**; *Bequaert 50* **6**; *Berg et al. P18679*! **1a**; *Bernardi 849* **1a**, *1500* **1a**, *19222*! **2**, *19506*! **2**, *19582*! **2**, *2553*! **3**, *Bernoulli & Cario 2056* **1a**; *Berry 1036*! **1a**, *1080*! **1a**, *1588*! **5**, *922*! **1a**, *1185*! **1a**, *1205*! **1a**; *Beuther 102*! **3**; *Billiet & Jadin 1060* **1a**, *1791* **1a**, *4814* **1a**; *Black 48-2937* **1a**, *48-3435* **1a**, *48-8432* **1a**, *49-8432* **1a**; *Black & Foster 48-3382* **1a**, *48-3405* **1a**; *Black & Magalhaes 51-12886* **1a**; *Black et al. 54-16530* **1a**, *54-17579* **1a**, *54-17623* **1a**; *Blackmore 3722* **4**, *4020* **1a**; *Blanco 1285* **1a**; *Blum & Dwyer 2130*! **1a**; *Boege 3241* **3**; *Bond et al. 205* **1a**; *Bonet 29* **1a**, *31* **3**; *Bonpland 39416*! **1a**; *Boom 4758* **1a**, *7156*! **1a**, *8520*! **1a**; *Boom & Grillo 6148*! **1a**, *6545*! **1a**; *Boom & Marín 10365* **1a**; *Bourgeau 1407*! **1a**; *Brandbyge & Asanza 31605*! **1a**; *Bravo 460* **6**; *Bredemeyer 180* W **1a**, *s.n.* **1a**, *s.n.* **3**; *Breedlove 24607* **1b**, *24694* **1b**, *26915*! **3**, *27312* **1a**, *36550*! **3**, *37262*! **3**, *39635*! **3**, *39856*! **3**, *51901*! **3**, *9946* **1b**; *Brenes 15567* **4**, *15598*F **4**, *15607* **4**, *22461* **1a**, *22462pp* **4**, *22464* **1a**, *22817* **4**, *3873* **4**, *HNCR14317* **4**; *Breteler 4019* **1a**, *4215*! **1a**, *5155* **1a**; *Brewer 58* **1a**; *Broadway 2556* **1a**, *648* **1a**, *676* **1a**, *7621*! **1a**, *7825* **1a**, *s.n.* **1a**; *Brunt 2244* **6**; *Buchtien 1322* **5**; *Bunting 11621* **1a**, *4297*! **1a**, *5319*! **1a**, *5333*! **3**, *5514A*! **1a**, *5514F* **1a**, *5620*! **3**, *7866*! **3**, *8817*! **1a**, *9019*! **3**, *9152*! **1a**, *9428*! **1a**; *Bunting & Alfonzo 8018*! **1a**,

9783 **3**, *9787* **3**; *Bunting & Fucci 7991* **3**, *7996* **3**; *Bunting & León 12573* **1a**; *Bunting & Licht 1286* **1a**; *Bunting & Licht 825* **1a**; *Bunting & Stoddart 9191* **3**; *Burger & Burger 7862* **1b**, *8461* **1a**; *Burger & Gentry 9167* **1a**; *Burger & Stolze 4861* **4**, *4866* **4**.

Cabrera 11453 **6**, *4121* **6**, *4262* **4**, *Cabrera & Cabrera 15221* **3**; *Cabrera et al. 2575* **6**; *Callejas et al. 4444* **1a**, *5036* **1a**, *5125* **1a**; *Calzada 640* **4**, *788* **1a**, *978* **4**; *Calzada et al. 6693* **3**, *6769* **3**, *6792* **3**; *Camby s.n.* **1a**; *Camp E-3812* **2**, *E-3892* **2**; *Canela s.n.* **1a**; *Cantin s.n.* **1a**; *Cárdenas de Guevara 1532* **3**, *2156* **1a**; *Cardona 1134* **1a**, *150* **1a**, *164* **1a**, *1669* **1a**, *2376* **1a**, *4054* **3**, *428* **1a**, *9* **1a**, *919* **1a**, *920* **1a**; *Carlson 1508* **1a**; *Carnevali & Lobo 663* **1a**; *Carrasquilla & Taymes 140* **1a**; *Castellanos 26930* **2**; *Castillo & Tapia 658* **4**; *Castillo 1484* **3**; *Cavalcante 1901* **1a**, *444* **1a**, *869* **1a**, *901* **1a**; *Cedillo & Torres 1089* **1a**; *Chacón & Chacón 2031* **1b**; *Chaffanjon 153* **1a**; *Chaing 234* **6**; *Chan 1145* **3**, *1393* **3**, *1823* **3**, *191* **6**; *Chan & Burgos 1417* **6**, *1452* **6**, *336* **4**; *Chan & Ucan 839* **6**, *942* **3**; *Chanek 201* **6**; *Chavarria 1001* **3**, *189* **3**, *261* **3**, *781* **4**, *825* **3**; *Chiang 340* **4**, *726* **1a**; *Cid & Nelson 2936* **5**; *Cid et al. 110* **1a**, *197* **1a**, *2025* **1a**, *507* **1a**, *5139* **1a**, *8467* **1a**; *Cisneros 81* **3**; *Clewell & Cruz 4028* **1a**; *Colella et al. 1046* **1a**, *1048* **1a**; *Combs 332* **3**; *Conggryp 120(40)* **1a**; *Contreras 4364* **4**, *5859* **3**, *8515* **6**, *8583* **4**, *900* **4**, *933* **4**, *965* **6**, *9743* **3**, *s.n.* **4**; *Conzatti et al. 3134* **1a**; *Coradin & Cordeiro 651* **1a**; *Córdoba 380* **1a**; *Cornelio 95* **3**; *Correa & Escobar 1788* **1a**; *Cowan 3022* **6**; *Cowell 189* **1a**, *78* **1a**; *Cremers 5025* **1a**, *5227* **1a**, *6678* **1a**, *6916* **1a**, *7193* **1a**, *7194* **1a**, *7270* **1a**, *7276* **1a**, *7361* **1a**, *7533* **1a**, *7537* **1a**, *7811* **1a**, *8092* **1a**, *8410* **1a**, *8445* **1a**; *Croat 10324* **1a**, *10798* **1a**, *11610* **1a**, *12268* **1a**, *12645* **1a**, *12796* **1a**, *12957* **1a**, *13487* **1a**, *14482* **4**, *14499* **4**, *15356* **1a**, *25188* **1a**, *42276* **3**, *42506* **3**, *43672* **3**, *43749* **3**, *4764* **1a**, *5119* **1a**, *5162* **1a**, *5208* **1a**, *5426* **4**, *5439* **1a**, *55333* **3**, *5589* **1a**, *5611* **1a**, *5700* **1a**, *6143* **1a**, *6155* **1a**, *6169* **1a**, *7176* **1a**, *8310* **1a**, *8552* **1a**, *8755* **1a**, *9514* **1a**, *9566* **1a**, *9776* **4**, *9846* **1a**; *Croizat 300* **1a**, *856C* **1a**; *de la Cruz 1455* **1a**, *1866* **1a**, *1992* **1a**, *3210* **1a**, *3798* **1a**, *4242* **1a**; *Cuadros 1109* **3**, *1384* **3**, *1683* **1a**, *3006A* **1a**, *3597* **1a**, *4492* **1a**; *Cuadros & Gentry 3006A* **1a**, *3050* **1a**, *3083* **1a**; *Cuatrecasas 7491* **1a**; *Cuevas & Guzmán 2933* **1a**; *Cumana 397* **1a**; *Cuming 1262pp* **4**; *Curran & Haman 1322* **1a**.

Daly & Cardoso 3918 **1a**; *Daly et al. 1406* **1a**, *4332* **1a**, *7156* **1a**; *Danin 76-14-4* **3**; *Darwin 2369* **3**; *Daubenmire 20J* **3**, *701J* **4**, *711J* **4**, *770J* **4**; *Davidse 15318* **1a**, *27891* **1a**, *34302* **4**; *Davidse & González 12196A* **1a**, *13860* **1a**; *Davidse & Huber 15318* **1a**; *Davidse et al. 17816* **1a**, *18202* **1a**, *18391* **1a**; *Deam 6309* **1b**; *De Martino et al. 016* **1a**; *DeLeón 1711* **4**; *Delascio 2164* **1a**; *Delascio & Guánchez 10943* **1a**; *Delascio Chitty 2448* **1a**; *de Nevers 4634* **1a**; *Devia 541* **3**; *Díaz & Jaramillo 1515* **1a**, *1517* **1a**, *1518* **1a**; *Diaz & Jaramillo 1526* **1a**; *Diaz et al. 1037* **1a**; *Dodge 10715* **1a**, *16570* **4**, *3507* **1a**; *Dodson & Gentry 9934* **2**; *Dodson 11520* **2**; *Dodson et al. 6964* **2**, *8851* **2**; *Dorantes 515* **4**, *548* **4**; *Dorantes et al. 5155* **4**, D-3167 **4**; *dos Santos 292* **1a**; *dos Santos et al. 119* **1a**, *127* **1a**, *129* **5**, *13* **5**, *132* **1a**, *134* **1a**, *17* **5**, *254* **1a**, *256* **1a**, *267* **1a**, *283* **1a**, *284* **1a**, *285* **1a**, *286* **1a**, *301* **1a**, *302* **1a**, *303* **1a**, *304* **1a**, *312* **1a**, *337* **1a**, *348* **1a**, *49* **5**, *86* **5**; *de Duchassaing 1851* **1a**; *Ducke s.n.* **1a**; *Dugand 1107* **3**, *434* **1a**, *4553* **3**, *5034* **3**, *6052* **1a**, *6338* **1a**, *6412* **1a**; *Dugand & Jaramillo 3278* **1a**, *3433* **1a**, *3434* **1a**, *3435* **1a**, *3500* **1a**; *Dugand & Seibert 1111* **3**; *Duke 10993* **1a**, *12268* **1a**, *14256* **1a**, *4696* **1a**, *4922* **1a**, *4978* **1b**, *4989* **1a**, *5531* **1a**, *5777* **1a**, *9700* **1a**; *Dunn et al. 23095*, **6**; *Duque-Jaramillo 4362A* **1a**; *Duran 224* **1a**, *10144A* **6**, *10710* **1a**, *11051* **1a**, *12562* **1a**, *12663* **6**, *12722* **6**, *12810* **1a**, *1334* **1a**, *21663* **6**, *4045* **1a**, *5130* **1a**, *8528* **1a**; *Dwyer & Kirkbride 7438* **1b**, *Dwyer & Pippin 10114* **6**, *10144App* **6**, *10214* **6**; *Dwyer et al. 146* **6**; *Dya 17* **5**.

Ebinger 288 **1a**; *Edwards P-148* **1a**; *Edward P-359* **3**, *P-597* **4**, *P-630* **3**; *Eggers 13121* **3**, *13128* **3**, *13546* **3**, *15070* **2**, *2631* **1a**, *310B* **1a**; *Egler & Irwin 46031* **1a**; *Egler & Pires 47765* **1a**; *Ek 648* **1a**; *Ekman H11175* **1a**; *Elias 1484* **3**, *540* **3**; *Enríquez 558* **4**, *598* **6**, *739* **3**, *775* **4**; *Erlanson 38* **4**, *485* **1a**; *Ernst 1656* **1a**, *1839* **1a**; *Espina 1016* **3**, *535* **1a**, *535* **1a**; *Espina & Mosquera 2115* **1a**, *2118* **1a**; *Eyerdam 8868* **3**.

Fager & Ribos 639 **2**; *Feddema 1934* **1a**, *2028* **1a**; *Fernández 293* **3**; *Fernández & Susanna 8437* **1a**; *Fernández Casas & Molero 6147* **2**; *Fernández 307* **1a**, *359* **3**, *4127* **1a**, *6944* **1a**, *906* **5**; *Fernández-Alonso 8134* **3**; *Fernández-Pérez 20127* **1a**; *Feuillet 1583* **1a**; *Fiebrig 4814* **2**; *Fleury 631* **1a**; *Flora Falcón 709* **1a**, *733* **1a**; *Flores & Puch 9052* **6**; *Flores & Yam 9142* **3**; *Flores s.n.* **6**; *Florschutz & Maas 2618* C **1a**; *Foldats 9220* **1a**; *Folsom 1653* **1a**; *Fonnegra & Torrez 758* **1a**; *Fonseca 351* **1a**; *Fonseca & Onishi 1279* **1a**; *Forero 1762* **1a**; *Forero & Hernández 1578* **3**; *de Foresta 602* **1a**; *Fosberg 39410* **1a**; *Foster et al. 1444* **3**; *Foster et al. 1592* **1a**; *Foster 933* **1a**; *Fournet 246* **1a**; *Frankie 408* **1b**, *441* **3**; *von Friedrichsthal 546* **1a**; *Froes 1839* **1a**, *28509* **1a**, *30991* **1a**, *30991a* **1a**, *31914* **1a**, *32347* **1a**, *32537* **1a**, *32729* **1a**, *34466* **1a**, *34607* **1a**, *34610* **1a**, *35607* **1a**; *Froes & Black 24517* **1a**, *24633* **1a**, *27486* **1a**, *27635* **1a**; *Fryxell & Anderson 3444* **6**; *Funck 294* **1a**; *Funck & Schlim 711* **1a**.

Gagzo s.n. **1a**; *Gandara & Dorantes 16* **4**; *García 51* **3**; *García-Barriga 10761* **1a**, *12166* **1a**, *13410* **3**, *13462* **3**, *6466* **1a**; *García-Barriga & Jaramillo 20561* **1a**; *García-Barriga & Lozano 18359* **1a**; *Garibaldi 235* **1a**; *Garner 4* **1a**; *Garnier 4332* A, **3**; *Gaumer 1966* **3**, *23818* **3**, *23888* **6**, *24024* **6**, *24267* **3**, *24298* **3**, *24345* **6**, *725pp* **6**, *751* **4**; *Gaumer et al. 725* **3**, *795* **3**; *Gentle 1080* **6**, *1259* **6**, *441* **6**, *543* **6**, *5577* **6**, *7562pp* **6**, *8794* **6**; *Gentry 10316* **3**, *1195* **1a**, *12519* **1a**, *1270* **1a**, *1271* **1a**, *1276* **1a**, *1279* **1a**, *12854* **1a**, *13261* **1a**, *1345* **1a**, *1350* **4**, *1414* **1a**, *14247* **1a**, *14285* **1a**, *14364* **1a**, *14833* **1a**, *1570* **1a**, *1583* **1a**, *1604* **1a**, *16119* **1a**, *1619* **4**, *16281* **1a**, *1779* **4**, *1811* **1a**, *19592* **1a**, *2055* **1a**, *2198* **1a**, *2204* **4**, *2219* **4**, *2229* **1a**, *2256* **4**, *2267* **1a**, *2274* **4**, *2359* **4**, *24801* **1a**, *2562* **1a**, *2564* **4**, *2615* **4**, *2629* **1a**, *28186* **1a**, *29508* **1a**, *301* **4**, *306* **3**, *306A* **3**, *3144* **1a**, *32310* **6**, *32504* **4**, *3282* **1a**, *3711* **1a**, *37593* **1a**, *3817* **4**, *384* **4**, *3859* **1a**, *3957* **1a**, *4020* **4**, *4059* **4**, *4088* **4**, *40922* **1a**, *40959* **1a**, *4116* **1a**, *41235* **1a**, *41326* **5**, *41685* **1a**, *4206* **4**, *431* **1a**, *4410* **1a**, *4420* **4**, *44983* **5**, *45101* **5**, *4539* **4**, *4564* **1a**, *4580* **1a**, *46257* **5**, *46475* **1a**, *47302* **1a**, *47478* **1a**, *47492* **3**, *47502* **1a**, *47618* **1a**, *47656* **3**, *482* **4**, *48611* **1a**, *4967* **4**, *4970* **1a**, *50384* **1a**, *50609* **1a**, *51222* **1a**, *5126* **4**, *51421* **1a**, *537* **3**, *54049* **1a**, *54102* **1a**, *56373* **1a**, *5726* **1a**, *5758* **1a**, *59285* **2**, *59301* **2**, *60581* **3**, *60654* **5**, *60737* **1a**, *61652* **5**, *62974* **1a**, *63360* **1a**, *63956* **1a**, *6494* **1a**, *6609* **1a**, *66161* **2**, *68146* **4**, *68250* **1a**, *68253* **3**, *68623* **5**, *68924* **5**, *69106* **1a**, *69145* **1a**, *69814* **1a**, *70274* **5**, *70503* **5**, *70713* **2**, *70828* **1a**, *70878* **5**, *710* **1a**, *71485A* **1a**, *71952* **3**, *72062* **3**, *72132* **5**, *72368* **2**, *72633* **2**, *73008* **2**, *73009* **2**, *73439* **1a**, *7454* **4**, *75599* **5**, *7585* **1a**, *7597* **1a**, *7620* **4**, *766* **4**, *77391* **1a**, *7815* **6**, *7851* **4**, *79290*

4, *79383*[1] **6**, *794* **3**, *79610* ? **1a**, *798* **4**, *812* **1a**, *815* **1a**, *8150*[1] **4**, *8177* **6**, *826* **1a**, *8262*[1] **6**, *8270* **3**, *829* **3**, *8311*[1] **6**, *8318* **3**, *8339*[1] **6**, *836* **1a**, *8360*[1] **6**, *841* **1a**, *844* **3**, *847* **3**, *860* **4**, *863* **3**, *880* **3**, *881* **3**, *884* **1a**, *887* **4**, *888* **3**, *892* **1a**, *9404*[1] **1a**, *9423*[1] **1a**, *9429*[1] **1a**, *9447*[1] **1a**, *9744*[1] **1a**; *Gentry & Aronson 25049*[1] **1a**; *Gentry & Berry 14516*[1] **1a**, *14527*[1] **1a**, *14698*[1] **1a**, *14771*[1] **3**, *14917*[1] **5**, *14987*[1] **1a**; *Gentry & Cuadros 47478* **1a**, *47492* **3**, *47656*[1] **3**, *63946* **1a**, *68253* **3**; *Gentry & Curso de Posgrado 68623*[1] **5**, *68924*[1] **5**; *Gentry & Daly 18914*[1] **1a**; *Gentry & Dwyer 3390* **1a**, *4827*[1] **1a**; *Gentry & Estensoro 70503* **5**; *Gentry & Forero 15359*[1] **1a**, *15396*[1] **1a**, *15460*[1] **3**, *15462*[1] **3**; *Gentry & Cuadros 47502*[1] **1a**; *Gentry & Gilly 10724* **4**; *Gentry & Jaramillo 57887*[1] **5**; *Gentry & Josse 72368* **2**; *Gentry & Josse 72633* **2**; *Gentry & Juncosa 40959*[1] **1a**; *Gentry & Núñez 66031*[1] **5**, *69610*[1] **1a**; *Gentry & Pinheiro 13096*[1] **1a**; *Gentry & Puig-Ross 14247*[1] **1a**, *14267*[1] **1a**; *Gentry & Puig-Ross 14364*[1] **1a**; *Gentry & Ramos 12925*[1] **1a**, *13339*[1] **1a**; *Gentry & Revilla 16667*[1] **1a**, *61119* **1a**; *Gentry & Smith 45101*[1] **5**; *Gentry & Tyson 1642*[1] **1a**, *4854*[1] **1a**; *Gentry & Vásquez 46257*[1] **5**; *Gentry & Young 31839*[1] **5**; *Gentry & Zardini 50384* **1a**; *Gentry et al. 10427*[1] **1a**, *10452*[1] **5**, *10641* **5**, *10644* **1a**, *10673*[1] **5**, *10737*[1] **5**, *10922*[1] **1a**, *10978*[1] **3**, *11042*[1] **1a**, *11116*[1] **1a**; *11160*[1] **1a**, *18077*[1] **1a**, *18095*[1] **1a**, *18097*[1] **3**, *18155*[1] **1a**, *18662*[1] **1a**, *25213*[1] **1a**, *25960*[1] **1a**, *27217*[1] **5**, *32311*[1] **6**, *34799A*[1] **4**, *37593* **1a**, *37648*[1] **5**, *38145*[1] **1a**, *51222* **1a**, *51421*[1] **1a**, *54049* **1a**, *5410*[1] **1a**, *56373* **1a**, *60581*[1] **3**, *61652*[1] **5**, *63360* **1a**, *69106*[1] **1a**, *71485-a* **1a**, *73884*[1] **2**, *7526*[1] **1a**, *76931*[1] **1a**, *77759*[1] **1a**, *8972*[1] **3**, *8973*[1] **3**; *Gillespie 1198*[1] **1a**, *2125*[1] **1a**, *2188*[1] **1a**, *2348*[1] **1a**; *Gilmartin 663* **2**, *665* **2**; *Ginés 4518* **1a**, *5100* **1a**, *5150* **1a**; *Glaziou 9951* **1a**; *Goeldi s.n. MG398* **1a**; *Goldman 1861* **1a**; *Gómez-Pompa & Riba 196* **6**; *González & Ortega 1358* **1a**; *González 74* **4**; *González-Ortega 1176* **1a**; *Gorts - van Rijn et al. 478*[1] **1a**; *Grández 860*[1] **1a**; *de Granville 5111*[1] **1a**, *5355*[1] **1a**, *5378pp* **1a**, *5765* **1a**, *9156*[1] **1a**, *B-4806*[1] **1a**, *B-5001*[1] **1a**; *de Granville et al. 10010* **1a**, *9590* **1a**, *9650*[1] **1a**, *9877*[1] **1a**, *9952*[1] 1; *Grayum 4251* **3**, *4636*[1] **4**; *Gregg 1033*[1] **1a**; *Grenand 2074* **1a**, *2088*[1] **1a**, *220* **1a**; *Grewal & Persaud 128* **1a**; *Grewal & Persaud 179* **1a**; *Grijalva 1024*[1] **3**, *1220*[1] **3**, *2151* **3**, *857* **3**; *Guagliumi 13* **3**; *Guánchez et al. 4216*[1] **1a**; *Gudino 1119*[1] **1a**, *1351* **1a**; *Guedes MG2293* **1a**; *Guedes 7* **1a**; *Guillen 2404Z* **1a**; *Guillet 711* **1a**, *712* **1a**; *Guppy & Lindeman 80* **1a**; *Gustafson 1450* **3**; *Gutiérrez 25* **3**; *Guzman & Montiel 337* **1b**; *Guzmán et al. 1079*[1] **3**, *1104*[1] **3**, *343*[1] **3**, *370*[1] **3**, *382*[1] **3**, *575*[1] **3**.

Haenke 1407 **1a**; *Hahn 1329*[1] **2**, *666* **4**, *3524*[1] **1a**; *Hahn et al. 1329* **2**, *1333*[1] **2**; *Hammel 4579*[1] **1a**; *Hansen et al. 1549*[1] **6**; *Harley et al. 10760*[1] **1a**; *Harmon 2524*[1] **6**; *Harmon & Dwyer 3826*[1] **3**; *Harris 1135*[1] **1a**, *1171*[1] **1a**; *Harvard Course in Tropical Botany 67* **3**; *Hassler 10022* **2**, *10022a* **2**, *10432*[1] **2**, *5409* **2**; *Hatschbach 46153*[1] **2**; *Hatschbach & Zelma 49084*[1] **2**; *Haught 2249*[1] **1a**, *2295*[1] **3**, *3497* **2**, *3603*[1] **1a**, *6577* **3**; *Hayden 20*[1] **1a**; *Hayes 126*[1] **4**, *412pp* **1a**, *587* **1a**, *590* **1a**; *Hazlett 742* **3**; *Heithaus 173* **4**, *300*[1] **3**; *Heller 4447* **1a**; *Henderson 612*[1] **1a**; *Henderson & Ribamar 578*[1] **1a**, *612* **1a**; *Henrich 108*[1] **4**, *181*[1] **4**; *Henrich & Stevens 181* **4**; *Hensen 150*[1] **2**; *Herald & Clark 390* **1a**; *Heriberto 40* **1a**; *Hernández 1308*[1] **6**, *310*[1] **3**, *358*[1] **1a**; *Hernández & Dorantes 1812*[1] **4**; *Hernández 122* **1a**; *Heyde 395*[1] **1a**, *580*[1] **1a**; *Heyde & Lindeman 107*[1] **5**, *258*[1] **5**, *299*[1] **1a**; *Higgins 203*[1] **1a**, *207*[1] **1a**; *Hinds 1841* **1a**; *s.n.* **1a**; *Hinton et al. 11732* **1a**, *16213* **3**; *Hitchcock & Stanford 6901*[1] **6**; *Hoff 5711*[1] **1a**; *Hoff et al. 6614* **1a**; *Hoffman 1226*[1] **1a**; *Hoffman & Benjamin 575*[1] **1a**; *Hoffman et al. 739*[1] **1a**; *Hoffmannsegg s.n.* **1a**; *Holm & Iltis 281* **3**; *Holm & Iltis 669* **1a**; *Holm-Nielsen 19964* **1a**, *19967* **1a**, *19989* **1a**; *Holm-Nielsen et al. 19441* **1a**, *19964* **1a**, *19967*[1] **1a**, *19989*[1] **1a**, *21304* **1a**, *19941*[1] **1a**; *Holst 2289* **1a**, *2305*[1] **1a**; *Holst et al. 2305* **1a**; *Holton 604* **3**; *Hopkins et al. 675*[1] **1a**, *749*[1] **1a**; *Horner 115* **1a**, *148* **1a**, *189*[1] **1a**; *Horner et al. 115*[1] **1a**, *148*[1] **1a**, *189* **1a**, *244*[1] **1a**, *363*[1] **1a**; *Hostmann 701* **1a**, *s.n.* **1a**; *Hostmann & Kappler 1051*[1] **1a**; *Huber s.n.* **1a**, *s.n. MG1160* **1a**, *s.n. MG267* **1a**, *s.n. MG3826* **1a**, *s.n. MG3836* **1a**, *s.n. MG782* **1a**; *Huertas & Hernández 4082* **1a**; *Hufi et al. 2113* **1b**; *Humboldt & Bonpland 1078* **1a**, *s.n.* **3**.

Ibarra-Manríquez & Sinaca 1752[1] **6**; *Idrobo 1516* **3**, *1508* **3**; *Idrobo et al. 1319* **1a**; *Ijjasz-Madriz 478* **1a**; *Iltis 27284a* **3**; *Iltis & Nee 1469* **1a**; *Irwin et al. 48056* **1a**, *47425* **1a**, *47575* **1a**, *48055* **1a**, *48056* **1a**, *48789* **1a**, *48790* **1a**, *53349*[1] **1a**, *55529*[1] **1a**, *55544*[1] **1a**; *Isert s.n.* **1a**.

Jacquemin 2098[1] **1a**, *2344* **1a**, *2543* **1a**; *Jahn 1231* **1a**, *1260* **1a**, *494* **3**; *Jangoux & Bahia 948*[1] **1a**; *Janzen 10060* **3**, *10425* **4**, *11725* **1b**, *11825* **4**, *12050* **4**, *12286* **4**, *12307* **1a**, *12318* **4**, *12321* **1a**, *12329* **4**, *12335* **1b**, *12348* **1b**, *12352* **1b**, *12362* **4**, *T-31* **3**, *T-89* **3**, *s.n.* **4**; *Jaramillo 219* **3**, *6889* **1a**, *6892* **1a**, *9070* **1a**; *Jaramillo & Coello 2941*[1] **1a**, *4149pp* **1a**, *4227* **1a**, *4419pp* **1a**, *4442* **1a**, *4469* **1a**; *Jaramillo et al. 1214* **1a**, *417* **1a**; *Jaramillo-Mejía & Palacios 7870* **1a**; *Jaramillo-Mejía et al. 8061* **1a**; *Jardim 1925Z* **2**, *2494Z* **1a**; *Jiménez 1093* **3**; *655-34298* **1a**, *3355* **1a**, *508* **1a**, *545* **1a**, *587* **1a**, *972* **3**, *s.n.* **4**; *Johnson 242-73* **4**; *Johnston 812*[1] **4**, *831* **4**; *Judziewicz 4565* **1a**.

Kant 1[1] **3**; *Keeler 171* **3**; *Kelly 133* **6**; *Kenoyer 533* **1a**; *Khan et al. 1226* **1a**; *Killeen 5432Z* **1a**; *Killip 33955* **1a**; *Killip & Dugand s.n.* **3**, *2465EPA* **3**, *37532* **1a**; *Killip & Smith 14079* **3**, *27481* **1a**, *30469* **1a**, *30569* **1a**; *Killip & Tamayo 37057* **3**; *Killip et al. 38200*[1] **3**; *Kimber 1576* **1a**; *King 635* **1a**; *Kinloch 249* **1a**; *Klug 4268*[1] **1a**, *4310* **1a**, *594* **1a**; *Knight 69-87*[1] **1a**; *Koch 4908* **3**; *Kral 25028* **6**, *69355*[1] **3**; *Krebbs s.n.* **1a**; *Krukoff 1784* **1a**, *4942*[1] **1a**, *6482*[1] **1a**, *6945*[1] **1a**, *7068*[1] **1a**, *8837*[1] **1a**; *Kuhlmann 1383* **2**; *Kukle & Boom 60*[1] **1a**; *Kvist et al. 384*[1] **1a**.

Langenheim 3242 **3**; *Langlassé 137*[1] **1a**, *506*[1] **1a**, *739* P **1a**; *Larpin 958*[1] **1a**; *Lasseigne 4382*[1] **1a**; *Lasser 4330* **1a**; *Lasser & Foldats 3008* **1a**, *3042* **3**, *3050* **3**, *Laughlin 1631* **3**, *871* **1b**, *872* **4**; *Lawesson et al. 43463* **1a**, *44265* **1a**, *44346* **1a**; *Lazor 5460* **1a**; *Leavenworth 205*[1] **6**; *Lellinger & de la Sota 605* **1a**; *Lent 103* **1a**, *1202* **3**; *León 368*[1] **1a**, *18078* **3**, *3156* **3**, *6861* **3**; *Levy 38* **1a**; *Lewis 1865*[1] **1a**; *Lewis et al. 1865* **1a**, *6533* **1a**; *Licata et al. 47*[1] **3**; *Liebmann 11* **4**, *58* **6**, *7986pp* **4**, *7992*[1] **6**, *8019* **1a**, *8020*[1] **6**, *8026* **4**; *Liesner 1369*[1] **1a**, *16365A* **5**, *2243* **3**, *2342* **1a**, *2458* **3**, *2800* **3**, *3386* **3**, *4427* **1b**, *4596* **3**, *4801* **1a**, *4907* **4**, *5749*[1] **1a**; *Liesner & Funk 16365*[1] **5**; *Liesner & González 10695*[1] **1a**, *11068*[1] **1a**, *5816*[1] **1a**, *749* **1a**; *Liesner et al. 8201*[1] **3**, *8314*[1] **3**, *8321*[1] **1a**, *8442*[1] **1a**; *Lima 388-68* **1a**; *Lima 38868* **1a**; *Linares 1316* **3**; *Lindeman 6358* **1a**; *Lindeman et al. 96* **5**; *Linden 219* **4**, *220* **6**; *Liogier 19353* **1a**, *9043-1* **1a**; *Liogier et al. 33809* **1a**; *Lizot 75* **1a**; *Long 115* **1a**; *López 548*[1] **4**; *López et al. 1006* **6**; *López-Palacios 1784*[1] **1a**; *Lott 1025*[1] **4**, *372*[1] **6**; *Lott & Barth 1166*[1] **3**; *Lott et al. 456*[1] **1a**; *Lugo 2588*[1] **1a**; *Lundell 1489* **3**, *15949*[1] **4**, *16087*[1] **6**, *3447* **4**, *4007* **6**, *4008* S[1] **6**, *6141* **6**, *6971* **3**, *839*[1] **3**, *841*[1] **3**; *Lundell & Lundell 7347*[1] **6**, *7600* **6**, *7893* [1] **3**, *8000* **3**, *8077*[1] **3**.

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1a; *Marcano-Berti et al.* U **5**; *Marcks & Marcks 980* **6**; *Marín 101*[1] **1a**; *Martinelli 7078*[1] **1a**; *Martínez 89*[1] **3**; *Martínez-Calderón 1405*[1] **6**, *1425* **4**, *1934* **6**; *Martino 467*[1] **1a**; *Martius 2608* **1a**, *2679* **1a**, *s.n.* **1a**; *Marulanda 767*[1] **1a**; *Mathias & Taylor 5978*[1] **1a**, *6054*[1] **1a**; *Matuda 15631* **1b**, *16589* **6**, *16956* **3**, *16959* **3**, *17571* **1b**, *17776* **6**, *17823* **1b**, *17857* **1a**, *3278*[1] **6**, *3528*[1] **6**, *5631* **1a**, *5652* **6**; *Maury 6199* **6**; *Maxon & Harvey 6640* **4**; *McDaniel 11860*[1] **1a**; *McDowell 2131*[1] **1a**, *2197*[1] **1a**, *3270*[1] **1a**, *3334*[1] **1a**, *3339*[1] **1a**, *3712*[1] **1a**; *McKearin 65*[1] **3**; *McPherson 10913* **1a**; *19014* **1a**; *Miller 6480*[1] **1a**; *Milliken et al. 95*[1] **1a**; *Miranda 5229* **4**, *5484* **3**, *7214* **6**, *7748* **1b**, *7749* **1b**, *7983* **4**, *7984* **6**; *Mitchell 90* **6**; *Mocquerys s.n.* **1a**, *s.n.* **3**; *Molina 15479* **3**, *1798* **1a**, *2099* **1a**, *2901* **1b**, *33921*[1] **4**, *5204* **3**, *6657* **1b**, *6935* **6**, *7469* **3**, *7927* **1b**, *s.n.* **3**; *Molina & Molina 24691* **3**, *30745* **3**, *30872* **1b**, *30881*[1] **3**; *Molina & Barkley s.n.* **3**; *Montalvo 3290*[1] **3**, *3506* **3**, *3716*[1] **3**; *Moore 980* **2**; *Moraes 990*[1] **1a**; *Morales 1659*[1] **3**, *2560*[1] **1a**, *2576*[1] **1a**, *3278* **3**, *3351* **6**, *3353* **4**, *4029* **4**, *4126* **1a**, *4127* **4**, *4131* **4**, *4153* **1a**, *4710* **4**; *Moreno 10017*[1] **3**, *10054*[1] **3**, *10098*[1] **3**, *10405*[1] **4**, *10679*[1] **3**, *10798*[1] **3**, *11253*[1] **4**, *1205*[1] **3**, *13167*[1] **1a**, *13295*[1] **1a**, *13171A*[1] **1a**, *16643*[1] **3**, *16950*[1] **3**, *1762*[1] **3**, *1788*[1] **3**, *17923*[1] 3, *17961*[1] **4**, *18388*[1] **3**, *18546*[1] **3**, *18673*[1] **3**, *18722*[1] **3**, *18733*[1] **4**, *18741*[1] **3**, *18755*[1] **4**, *1935*[1] **3**, *21153* **1a**, *21449*[1] **4**, *21492*[1] **4**, *22515*[1] **3**, *22534*[1] **3**, *22613*[1] **3**, *22788*[1] **3**, *22887* **3**, *23533*[1] **4**, *23675*[1] **1a**, *2385*[1] **3**, *23946*[1] **1a**, *24243*[1] **1a**, *24428*[1] **3**, *24479* **1b**, *24480*[1] **4**, *3038*[1] **3**, *3464*[1] **3**, *3533*[1] **3**, *3626*[1] **3**, *3641*[1] **3**, *3789*[1] **4**, *3816*[1] **3**, *4210*[1] **3**, *4599*[1] **3**, *4625*[1] **4**, *4670*[1] **4**, *4772*[1] **3**, *5084*[1] **3**, *5375*[1] **4**, *5623*[1] **3**, *6603*[1] **1a**, *6797*[1] **3**, *9310*[1] **3**, *9400*[1] **3**, *9911*[1] **3**; *Moreno & Henrich 8458*[1] **4**; *Moreno & Robleto 22887*[1] **3**; *Moreno & Sandino 13295* **1a**, *6190*[1] **3**; *Mori & Kallunki 1785*[1] **1a**; *Mori & Gracie 22099*[1] **1a**; *Mori & Bolten 8443*[1] **1a**; *Mori & Cardoso 17730* **1a**; *Mori & Kallunki 1785* **1a**; *Mori et al. 21995*[1] **1a**, *22138*[1] **1a**, *14939*[1] **1a**, *14996*[1] **1a**, *15042*[1] **1a**; *Morillo & Liesner 8842*[1] **1a**; *Morillo et al. 4267*[1] **3**; *Mrs. J.J. Ricksecker 426*[1] **1a**; *Murillo & Jaramillo 219* **3**; *Mutis 4180* **1a**, *5638* **1a**, *929* **1a**.

Narváez 33 **3**, *83* **3**; *Narváez & Puch 448* **6**, *462* **6**; *Nassar 57* **3**; *Nee 10289*[1] **1a**, *11404*[1] **1a**, *11774*[1] **1a**, *27551* **4**, *28266*[1] **3**, *33480*[1] **2**, *33835*[1] **2**, *37959*[1] **5**; *Nee & Miller 27551*[1] **4**; *Neill 2411*[1] **3**, *2471*[1] **3**, *2645*[1] **3**, *3184*[1] **4**, *443*[1] **1a**, *4635*[1] **4**, *585* **1b**, *7304*[1] **1a**, *814* **3**; *Neill et al. 8264*[1] **1a**, *8315*[1] **1a**; *Nelson 634*[1] **1a**; *Nicolson 4198* **1a**; *Núñez 10167*[1] **1a**, *12796*[1] **5**, *12805*[1] **5**; *OTS s.n.* **3**.

Oersted 7957 **4**; *7960* **3**, *7965* **3**, *s.n.* **3**, *s.n.* **1a**, *s.n.* **1a**, *s.n.* **4**; *Oldeman 1375*[1] **1a**, *2220*[1] **1a**, *2368* **1a**, *3028*[1] **1a**, *B-1107*[1] **1a**, *B-1305*[1] **1a**, *B-2515*[1] **1a**, *B-3406*[1] **1a**, *B-524*[1] **1a**, *B-780*[1] **1a**, *B524* **1a**, *T-42* **1a**; *Oliveira 1209* **1a**, *1669* **1a**, *3424* **1a**, *3772* **1a**, *37772* **1a**, *4192* **1a**, *4337* **1a**, *4926* **1a**, *503* **1a**, *5243* **1a**, *5755* **1a**, *998* **1a**; *Ollgaard et al. 57183*[1] **1a**; *Opler 156* **4**, *1671* **3**, *1738* **1b**, *1745* **4**, *1764* **4**, *634* **3**, *642* **1b**, *832* **1b**, *969* **3**; *Ortiz 1175* **6**; *Otero M-19* **1a**; *der Outer 958* L **1a**; *Ozment et al. 453* **6**.

Palacio & Bautista 3299 **1a**; *Palmer 48pp*[1] **1a**, *587*[1] **1a**; *Pannier 835* **3**; *Para 80*[1] **1a**; *Paul 236* **1a**; *Paul et al. s.n.* (*779*) **1a**; *Pavez s.n.* **1a**; *Paz y Mino 81002*[1] **1a**; *Pedersen 12281*[1] **2**; *Pena 130* **1a**, *156* **1a**; *Pérez 1678*[1] **3**; *Pérez-Arbaláez & Cuatrecasas 6357* **1a**, *6400* **1a**; *Pére Duss 3065*[1] **1a**; *Philcox et al. 3327* **1a**; *Philipson et al. 2020* **1a**; *Pinto et al. 328* **1a**; *Pipoly et al. 13488*[1] **1a**; *Pipoly & Ameer 9273*[1] **1a**, *9277*[1] **1a**; *Pipoly & Lall 8247* **1a**, *8255* **1a**; *Pires 13218* **1a**, *51361* **1a**; *Pires et al. 50492* **1a**, *50872* **1a**; *Pittier 10278* **3**, *11885* **1a**, *11901* **3**, *12422*[1] **3**, *12454* **1a**, *15117* **1a**, *15539* **1a**, *15577* **1a**, *15585* **1a**, *16105* **1a**, *2576pp* **1a**, *2629* **3**, *2773* **1a**, *4766* **4**, *6056* **1a**, *6353* **1a**, *6762pp* **1a**, *6762pp* **4**, *7467* **3**, *7470* **3**, *7832* **1a**, *7900* **3**, *7901*[1] **1a**, *7946*[1] **3**, *7959*[1] **3**, *8095* **1a**, *8865* **1a**, *9067* **3**; *Plowman et al. 8878*[1] **1a**; *Porter 1144* **3**; *Prance 22452*[1] **1a**, *29875* **1a**, *s.n.* **1a**; *Prance & Pennington 1335*[1] **1a**; *Prance et al. 11893* **1a**, *13980*[1] **1a**, *14518*[1] **1a**, *18216*[1] **5**, *25895*[1] **1a**, *7513*[1] **5**, *7947*[1] **5**, *P25895* **1a**, *s.n.* **1a**; *Prevost 1080*[1] **1a**, *1395*[1] **1a**, *628*[1] **1a**, *795*[1] **1a**; *Pringle 3692*[1] **6**; *Procter 4785*[1] **1a**; *Proctor 30216* **6**; *Pruski et al. 2781* **1a**; *Psima 78* **3**; *Puch & Narváez 304* **3**; *Purpus 8791*[1] **4**.

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Sabatier 720 **1a**; *Saddi & Mattos Filho 3432* **2**, *3579* **5**, *3667* **5**; *Saer 251* **1a**, *522* **3**, *651* **1a**, *658* **3**; *Sagot 402* **1a**; *Sagra s.n.* **3**; *de la Sagra 33892*[1] **3**; *Saldias 3607* **1a**, *3817* **5**; *Samuels 68* **1a**; *Sanabria et al. 178* **1a**; *Sandeman 5919* **1a**; *Sanders 9838*[1] **6**; *Sandino 1365*[1] **1a**, *1396*[1] **3**, *1872*[1] **3**, *251*[1] **3**, *2591B*[1] **1a**, *2995*[1] **6**, *3229*[1] **3**, *4363* **4**, *919*[1] **1a**; *Sandino & Rodríguez 1431*[1] **3**; *Sanoja 1200*[1] **1a**; *Santos et al. 99*[1] **1a**; *Santos 149*[1] **1a**; *Saravia et al. 1001* **1a**; *Sastre 1431*[1] **1a**, *8114*[1] **1a**; *Sastre et al. 4143*[1] **1a**; *Sastre & Sastre 4158*[1] **1a**; *Sauer & Gade 3185* **3**; *Schipp 8453* **1a**; *Schnee 456* **1a**; *Schnell 11396*[1] **1a**, *12294*[1] **1a**; *Schomburgk 576* **1a**, *579* **1a**; *Schott 506* **3**; *Schott 354* **6**, *530* **3**; *Schubert & Pompa 1678* **4**; *Schunke 5755*[1] **1a**, *5762*[1] **1a**, *6379*[1] **1a**, *7966*[1] **1a**, *8130*[1] **1a**, *8529*[1] **1a**; *Seemann 397* **1a**, *601* **4**, *602* **1a**, *s.n.* **4**; *Seibert 1664*[1] **1a**; *Seidel 117*[1] **2**; *Seidel & Beck 213*[1] **2**; *Seler 5551* **6**; *Serv. For. Cayenne 3803* **1a**, *7781* **1a**; *Sessé & Mociño 2395* **1a**, *2406* **3**; *Shannon 5048* **1a**, *5049* **1a**; *Shattuck 1040*[1] **1a**, *1147*[1] **1a**, *784pp*[1] **4**; *Silva 159*[1] **1a**, *713* **1a**, *134773* **1a**, *1619* **1a**, *2326*[1] **1a**, *2359* **1a**, *2586*[1] **1a**, *2908* **1a**, *933* **1a**; *Silva et al. AS102*[1] **1a**, *7109*[1] **1a**; *Silverstone 2572* **1a**, *2658*[1] **1a**, *3675* **1a**; *Silverstone-Sopkin 2658* **1a**, *5556*[1] **1a**, *6138*[1] **1a**; *Sinclair s.n.* **1a**; *Sintenis 1817* **1a**, *5616* **1a**, *945* **1a**; *Skinner 51* **3**, *53* **3**, *60*[1] **1a**, *66*[1] **3**; *Skog et al. 7439*[1] **1a**; *Smith 2537*[1] **1a**, *2710*[1] **1a**, *3382*[1] **1a**, *1386* **4**, *1143*[1] **1a**, *2515*[1] **1a**, *351*[1] **3**, *352*[1] **1a**, *355*[1] **3**, *738* **1a**, *s.n.* **3**, *1721* **1a**; *Smith & Hodgdon 3194*[1] **3**; *Solomon 2446* **3**, *610* **3**; *Solomon et al. 7016*[1] **2**; *Solymosy 7111* **3**; *Sonntag 17* **1a**; *Soria 2613*[1] **2**; *Soto Núñez & Silva 4510*[1] **3**; *Sousa 1759* **6**, *293pp* **1a**, *4497* **4**, *7285*[1] **6**; *Splitgerber 1089* **1a**, *130* **1a**, *309* **1a**; *358* **1a**; *Stahl 820* **1a**; *Standley 22061* **4**, *22119* **1b**, *27944* **1a**,

28628 **1a**, *28642* **1a**, *31183*[1] **1a**, *40027* **1a**, *64106* **6**, *73829* **3**, *9208* **3**, *9361* **1a**, *9362* **4**, *97* **3**; *Standley & Chacón 5239* **3**, *5945* **3**; *Standley & Padilla 3047* **3**, *3206A* **3**; *Standley & Valerio 46564* **1a**; *Steere 1061* **3**, *1366*[1] **3**, *1606* **6**, *2055* **3**, *2273* **3**, *2338* **3**, *2340* **3**, *3007* **3**, *7704* **3**; *Steggerda 18* **3**; *Stergios 10051* **1a**, *10776* **1a**, *10780* **1a**, *11069* **1a**, *6952*[1] **3**, *7029*[1] **1a**; *Stergios & Aymard 4182*[1] **1a**; *Stergios & Delgado 12926* **1a**; *Stergios & Stergios 11333* **1a**, *8440*[1] **1a**; *Stergios et al. 2687*[1] **1a**, *3341*[1] **1a**, *3914* **1a**, *3921*[1] **1a**, *3940*[1] **1a**, *5006A*[1] **1a**, *5285*[1] **1a**, *6034*[1] **1a**, *6041*[1] **1a**, *6109*[1] **1a**, *6115*[1] **1a**, *6144*[1] **1a**, *6151*[1] **1a**, *6160*[1] **1a**, *6166*[1] **1a**, *6184*[1] **1a**, *6256*[1] **1a**, *8169B*[1] **1a**, *8702*[1] **3**, *9378*[1] **1a**, *9392*[1] **1a**, *9627*[1] **1a**; *Stern 96*[1] **1a**; *Stern et al. 755* **1a**, *882* **1a**; *Stevens 11274*[1] **3**, *13597* **3**, *17418*[1] **1a**, *21785*[1] **3**, *22764B* **3**, *23050* **3**, *24012* **1a**, *24013* **1a**, *25020* **1a**, *2702*[1] **3**, *306* **3**, *307* **3**, *309* **3**, *317* **3**, *3872*[1] **3**, *4431*[1] **3**, *51* **3**, *52* **3**, *53* **3**, *5352*[1] **3**, *54* **4**, *5431*[1] **3**, *9537*[1] **3**, *9663*[1] **3**; *Stevens & Montiel 17142*[1] **4**; *Stevens et al. 16887*[1] **4**, *17229*[1] **1a**, *17286*[1] **4**, *20164*[1] **4**, *25020* **1a**, *Steyermark 108400*[1] **1a**, *39099* **1a**, *39686* **1a**, *45805* **6**, *87224* **1a**, *87729* **1a**, *88143* **1a**, *93143* **1a**, *98879* **3**, *98897*[1] **1a**; *Steyermark & Aristeguieta 113* **3**; *Steyermark & Berry 111806*[1] **3**; *Steyermark & Brewer 105275*[1] **1a**; *Steyermark & Delascio 129176*[1] **1a**; *Steyermark & Liesner 127419*[1] **1a**; *Steyermark & Manara 110761*[1] **3**, *110966*[1] **1a**; *Steyermark et al. 101516*[1] **1a**, *102105* **1a**, *114627*[1] **1a**, *114668* **1a**, *114721*[1] **1a**, *114743*[1] **1a**, *114807* **1a**, *120157*[1] **1a**, *123146*[1] **1a**, *123161*[1] **3**, *123406*[1] **1a**; *Stork 2795* **1a**, *4009* **3**; *Strudwick et al. 3932*[1] **1a**; *Suringar s.n.* L **1a**; *Svenson 417* **4**; *Swallen 2546* **6**, *2547* **6**.

Tamayo 2803 **1a**, *2853* **1a**, *3640* **1a**, *4426* **1a**; *Taylor 11156*[1] **1a**; *Taylor 4421* **3**; *Téllez 10365*[1] **1a**, *10369* **4**; *Téllez 2055*[1] **6**, *2223*[1] **6**, *2389* **6**, *2418*[1] **6**, *2470*[1] **6**, *2478*[1] **6**, *2518*[1] **4**, *2691*[1] **6**, *2863*[1] **3**, *3289*[1] **6**; *Téllez & Cabrera 2387* **4**, *2729* **6**; *Téllez & Martínez 971* **3**; *Thomas 3978*[1] **1a**; *Thomas et al. 5386*[1] **1a**; *Timaná & Astete 1674*[1] **5**; *Timaná & Jaramillo 2386* **5**; *Tonduz 13826* **1b**, *13912*, **1a**, *13883* **1a**, *2779* **1a**; *Torres & Torres 210*[1] **6**; *Torres 1347*[1] **3**, *1953* **1a**; *Torres & Abisai García 6828*[1] **3**; *Trott et al. 186*[1] **3**; *Trujillo 1740* **3**, *3784* **1a**, *4425* **1a**, *5288* **3**, *8525* **3**; *Trujillo & Fernández 399* **1a**; *Tsugaru & Sano B-540* **1a**; *von Tuerckheim 2527* **1a**; *Tulleken s.n.* **1a**; *Tun 1175*[1] **6**, *1211*[1] **6**, *1764* **4**, *1843*[1] **6**, *1907*[1] **6**, *1910* **4**, *1986*[1] **3**, *2616* **6**, *292* **3**; *Tyson 1089*[1] **1a**, *2683*[1] **1a**, *6638*[1] **1a**, *6805*[1] **1a**, *6888*[1] **1a**.

Ucan 108 **3**, *2315* **6**, *307* **6**, *598* **3**; *Ucan & Burgos 1188* **3**, *1354* **6**; *Ucan & Yam 1876* **3**; *Underwood & Griggs 261* **1a**; *Uribe-Uribe 1298* **1a**, *3631* **1a**, *551* **1a**.

Vahl s.n. **1a**; *Vaillant s.n.*[1] **1a**; *Valerio 47* **1a**; *Varela 44* **3**; *Vargas 7660*[1] **3**; *Vargas 145* **3**, *239* **6**, *34* **4**, *52* **6**; *Vargas & Seidel 2022*[1] **2**; *Vásquez 10040* **1a**, *1511*[1] **1a**; *Vásquez et al. V-756*[1] **4**; *Velasco 59* **3**, *86* **1a**; *Velázquez 295* **4**; *Ventura 11210* **4**, *11294* **4**, *11469* **4**, *11564* **4**, *12675* **4**, *12757* **4**, *13976* **4**, *20799*[1] **3**, *3728* **4**, *7750* **4**, *8077* **4**, *9423* **4**; *Ventura & López 3690*[1] **1a**; *Villiers & Feuillet 2022* **1a**; *Vogel 1269* **1a**, *389* **3**, *391* **1a**, *790* **3**, *973*[1] **3**, *982* **1a**, *s.n.* **1a**, *s.n. 389* **3**; *Vreden 11710* **1a**.

Warscewicz 51 **1a**; *Webster & Kennedy 16879*[1] **1a**; *Webster et al. 12722*[1] **3**; *von Wedel 2388*[1] **1a**, *2415*[1] **1a**, *2449*[1] **1a**, *2451*[1] **1a**, *2827*[1] **1a**, *554*[1] **1a**; *van der Werff 5345*[1] **1a**; *van der Werff & González 5345* **1a**; *West 3561*[1] **3**; *West 15* **1a**, *25/2* **1a**; *White 146*[1] **4**; *Whitmore 29* **3**; *Wilbur 26714* **3**; *Wilbur & Wilbur 1595* **1a**; *Williams 10308*[1] **3**, *10643* **1a**, *10845* **1a**, *10847* **1a**, *11446* **1a**, *12192* **1a**, *12531*, **1a**, *12648* **1a**, *13599* **1a**, *15346* **1a**, *15506* **1a**, *16097* **1a**, *9267* **1a**, *9833* **1a**, *9875* **1b**, *s.n.* **4**; *Williams et al. 26473* **1a**; *Williams 14119* **4**; *Williams & Molina 12577* **1b**, *14681* **3**; *Williams & Williams 18306* **3**; *Williams 228* **1a**, *624* **5**; *Woodbury 3403* **1a**; *Woodson 1196*[1] **1b**; *Woodson & Schery 1309*[1] **1a**, *1651*[1] **1a**, *1679* **1a**, *811A*[1] **1a**; *Woodson et al. 119* **1b**; *Woytkowski 35018*[1] **1a**, *6264*[1] **1a**; *Wright 3049*[1] **3**; *Wullschlaegel 2005* **1a**, *2005* **1a**, *2505 photo* **1a**; *Wurdack & Adderley 43075*[1] **1a**; *Wurdack & Monachino 41276* **1a**.

Yero 1046 **3**, *238* **3**; *Yjjasz 478* **1a**; *Yuncker 8262* **6**.

Zambrano 1389[1] **1a**; *Zamora 2118* **3**; *Zanoni & Mejía 9017* **1a**; *Zanoni et al. 21237* **1a**, *34268-A* **1a**; *Zardini 4125*[1] **2**; *Zarucchi 3859* **1a**, *4064* **1a**, *4126* **1a**, *5500* **1a**, *6465* **1a**; *Zarucchi & Betancur 6465*[1] **1a**; *Zarucchi & Cuadros 3859*[1] **1a**, *4064*[1] **1a**, *4126*[1] **1a**; *Zarucchi et al. 5500*[1] **1a**; *Zaruma 599*[1] **1a**; *Zuluaga 822* **1a**.

w/o collector 123 **1a**; w/o collector 55 **1a**; w/o collector 7148[1] **1a**.

Index to Scientific Names

Anemopaegma ... 815, 829
decorum ... 815, 828
tonduzianum ... 828
vargasianum ... 829
Arrabidaea ... 815, 833
decora ... 828
guatemalensis ... 828
isthmica ... 825
potosina ... 815, 833
pseudochica ... 828
Bignonia ... 815, 823, 825, 828, 829, 831, 834
aequinoctialis ... 815, 823
diversifolia ... 815, 829
hostmannii ... 825
incarnata ... 834
lepidota ... 831
nitidissima ... 825
picta ... 825
sagreana ... 829
sarmentosa ... 828
spectabilis ... 825
variabilis ... 834
villosa ... 825
Clytostoma ... 816, 817, 826, 828, 833, 834
decorum ... 828
mayanum ... 833
Clytostomanthus ... 815, 820, 828, 829
decorus ... 820, 828
Cydista aequinoctialis ... 815, 817–821, 823, 825, 828, 830, 833–835
aequinoctialis var. aequinoctialis ... 817, 823, 825
aequinoctialis var. hirtella ... 818, 820, 823, 825
amoena ... 815, 834
analoga ... 834
blanda ... 834
decora ... 817–821, 825, 828, 829, 834, 835
diversifolia ... 815, 817–819, 821, 825, 830, 835
eximia ... 834
heterophylla ... 815, 817, 818, 820, 821, 825, 830, 831, 834, 835
incarnata ... 815, 834
lilacina ... 815–819, 821, 823, 826, 832–835
magnifica ... 834
potosina ... 816, 817, 818, 821, 826, 830, 834, 835
pubescens ... 815, 828

rubicunda 834
sarmentosa 828
seemannii 815, 835
spectabilis 815, 825
vargasiana 815, 829
Levya 815, 820, 828
nicaraguensis 820, 828
Mansoa 815
difficilis 815
Phryganocydia 817, 826
Pleonotoma 815, 829
diversifolium 829
Potamoganos 817, 826
Roentgenia 815–817, 826
bracteomana 815
Temnocydia 815, 823, 825
aequinoctialis 823
spectabilis 825

SYSTEMATICS OF *ELEUSINE* GAERTN. (POACEAE: CHLORIDOIDEAE): CHLOROPLAST DNA AND TOTAL EVIDENCE[1]

Khidir W. Hilu[2] *and John L. Johnson*[3]

Abstract

Eleusine (Poaceae) comprises four annual and five perennial species, which are primarily East African except for the vicariant *E. tristachya*, a widely distributed species in South and Central America. Taxonomic difficulties in the genus have been attributed to active speciation in the early stages. *Eleusine* includes an allotetraploid African and Indian cereal, *E. coracana* subsp. *coracana*, a taxon with an incompletely resolved origin. Chloroplast DNA restriction site variation is used here to elucidate the phylogenetic relationships among species of *Eleusine*, assess the affinity of *E. multiflora* to the genus, and provide additional input into the origin of polyploid *E. coracana*. Chloroplast DNA data confirm the monophyly of the annuals *E. coracana*, *E. indica*, and *E. tristachya* and support the inclusion of the annual *E. multiflora* in the genus as a separate entity. The perennial species appeared paraphyletic. Information from the chloroplast genome is in general agreement with previous molecular, biochemical, and cytogenetical studies on the genus. The present investigation provides additional support for the origin of the crop from the tetraploid *E. coracana* subsp. *africana* and substantiates the monophyly of the two subspecies of *E. coracana* and *E. indica*. Evidence presented points to the African origin of the vicariant *E. tristachya* and an earlier introduction to and further differentiation in South America.

Eleusine Gaertn., Poaceae subfamily Chloridoideae, is comprised of four annual and five perennial species (Phillips, 1972). Polyploidy (both euploidy and aneuploidy) has played a role in the evolution of the genus with the evident presence of diploids and polyploids based on basic chromosome numbers of $x = 10$, 9, and 8 (Hiremath & Chennaveeraiah, 1982; Hiremath & Salimath, 1991). Clayton and Renvoize (1986) indicated that active speciation has made the genus taxonomically difficult. *Eleusine* has a center of diversity in East Africa where eight of its nine species occur. The exception is *E. tristachya* (Lam.) Lam., which occurs from South America north to the southwestern United States, and as a rare adventive in East Africa (Hilu, 1980).

Phillips (1972) arbitrarily divided *Eleusine* into two groups, annuals and perennials. Among annuals, the taxonomic affinity of *E. multiflora* Hochst. ex A. Rich. to the other species was questioned originally on the basis of morphological information (Phillips, 1972; Hilu & deWet, 1976a). However, isozyme information (Werth et al., 1994) points to close affinity between *E. multiflora* and other species of *Eleusine*. The remaining annual taxa include *E. coracana* (L.) Gaertn. subsp. *coracana*, an important East African and Indian crop known as finger millet. The crop is believed to have been domesticated from *E. coracana* subsp. *africana* (Kennedy-O'Byrne) Hilu & deWet (Chennaveeraiah & Hiremath, 1974; Hilu, 1988). Isozyme information, on the other hand, raised the point that subspecies *africana* may not be the direct ancestor of the crop (Werth et al., 1994). This hypothesis and the unknown identity of one of the diploid parents leave unresolved questions about the origin of tetraploid *E. coracana*.

Among the perennials, *E. semisterilis* S. M. Phillips has been described from a single specimen collected from the southeastern part of Kenya, near Mombasa (Phillips, 1972), and possibly has become extinct. The remaining perennial species have wider geographic distributions in East Africa.

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[2] Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, U.S.A.

[3] Department of Biochemistry, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, U.S.A.

Table 1. Species, chromosome numbers, plant collections used in the study, and sources of the material. The PI numbers refer to the U.S. Department of Agriculture collections (USDA), and the KH numbers designate K. Hilu collections. Voucher specimens are located at VPI.

Species	Collection number	Geographic origin	Chromosome number ($2n$)
Eleusine coracana subsp. *coracana*	USDA, PI231130	Fort Portal, Uganda	36
E. coracana subsp. *africana*	USDA, PI315700	Pretoria, South Africa	36
E. indica	USDA, PI231130	Nilgiri Hills, India	18
E. tristachya	KH2414	Uruguay	18
E. multiflora	KH258	Rift Valley, Kenya	16
E. jaegeri	KH221	Narok, Kenya	20
E. floccifolia	USDA, PI196853	Addis Ababa, Ethiopia	18
Dactyloctenium aegypticum	Hilu, KH263	Eldorat, Kenya	—

Phylogenetic relationships among the perennial species have not been examined.

The objectives of this chloroplast DNA study are to elucidate the phylogenetic relationships among species of *Eleusine*, evaluate the proposed infrageneric grouping of the species, provide information on the origin of the New World species *E. tristachya*, assess the affinity of *E. multiflora* to *Eleusine*, and provide additional insight into the origin of polyploid *E. coracana*.

Materials and Methods

Chloroplast DNA (cpDNA) was isolated from plants grown in the greenhouse. The species, seed collections, and sources of material for *Eleusine* and the outgroup *Dactyloctenium aegyptium* (L.) P. Beauv. are listed in Table 1. *Dactyloctenium* Willd. and *Eleusine* are members of the subtribe Eleusininae and are considered to be taxonomically linked (Clayton & Renvoize, 1986). Plant material for *E. intermedia* S. M. Phillips and *E. kigeziensis* S. M. Phillips was not available. A previous study on the cpDNA variation in *Eleusine* (Hilu, 1988) demonstrated the lack of infraspecific variability; thus one collection per taxon was used here.

Seeds were grown in flats and leaves were harvested from 5–7-inch seedlings, frozen in liquid nitrogen, and stored at −70°C. DNA was isolated following the procedure of Saltz and Beckman (1981) as modified in Hilu (1988). The DNA was digested with the restriction endonucleases *Ava*I, *Ava*II, *Bam*HI, *Bcl*I, *Bgl*II, *Dra*I, *Eco*RI, *Ssp*I, *Pst*I. The DNA fragments were resolved electrophoretically on 0.8% agarose gels, stained in ethidium bromide, and photographed in UV light. For the Southern hybridization, DNA was transferred to Zetaprobe nylon membranes (BioRad Inc.) using the alkaline procedure (Reed & Mann, 1985). The membranes were baked in an oven at 65°C for 2 hours and stored at 4°C.

To examine the restriction sites in the cpDNA, ten *Pst*I cloned cpDNA fragments of barley (provided by T. H. N. Ellis and A. Day) covering 98% of the genome (Day & Ellis, 1985) were used sequentially as hybridization probes. The probes were labeled with ^{32}P using the nick translation kit of Bethesda Research Laboratories Inc. (BRL). The membranes were prehybridized overnight at 65°C in 3× SSC, 20 mM phosphate buffer pH 7.0, 7% SDS, 10× Denhardt's solution, and 100 mg/ml salmon sperm DNA. Identical conditions were used for probe hybridization. Membranes were exposed to Kodak XAR-5 film to visualize homologous bands. Probe stripping was carried on after each hybridization by washing the membranes three times, 20 min. each, in 0.1× SSC and 0.5% SDS at 95°C. DNA fragment sizes were calculated by comparison to Lambda *Hin*dIII and a 1-kilobase fragment ladder marker (BRL).

Phylogenetically informative sites (i.e., those found in two or more but not all species) were scored as present-absent. Small deletions and additions unique to particular taxa were excluded from the analysis. The data were polarized in relation to the outgroup species *Dactyloctenium aegyptium*, transformed into NEXUS format using MacClade 3.0 (Maddison & Maddison, 1992), and analyzed by the Wagner parsimony method in PAUP version 3.0 (Swofford, 1990). The parsimony analyses were conducted using the exhaustive search method with MULPARS, TBR branch swapping, and CLOSEST addition to estimate relationships and tree topology. The bootstrap method with 100 replications and the branch-and-bound search,

Table 2. Restriction site mutations detected in the cpDNA of *Eleusine* species. The position of the restriction site on the chloroplast genome is identified by the probe used (P1–P7) and the restriction enzyme (see Day & Ellis, 1985, for probes map). When more than one restriction site is revealed by a probe, the sites are designated by an alphabetical letter.

	*Eco*RI		*Ssp*I			*Bam*HI				*Ava*I		*Ava*II			*Dra*I	
	P1	P2	P3a	P3b	P4	P1	P4a	P4b	P7b	P1	P2	P1a	P1b	P5	P1	P2
coracana	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0
indica	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0
tristachya	1	0	0	0	0	1	1	0	0	0	0	1	1	1	1	0
multiflora	0	1	1	0	1	0	1	1	0	1	1	0	1	1	1	1
jaegeri	0	1	1	1	0	1	1	0	0	1	1	1	0	0	1	1
floccifolia	0	1	0	0	1	1	1	0	1	1	1	1	1	1	0	0
Dactyloctenium	0	1	0	1	1	0	1	1	1	1	1	0	0	0	0	1

and the decay analysis were performed in PAUP to determine relative support for the clades (Felsenstein, 1985; Bremer, 1988).

Results

Hybridization of the cpDNA clones to the restriction digests of the *Eleusine* species revealed 28 restriction sites. Sixteen sites were phylogenetically informative, while the remaining 12 were present in only one species (Table 2). Ten of the unique sites were characteristic of the *E. multiflora* genome, one was found in *E. floccifolia* (Forssk.) Spreng., and the other occurred in *Dactyloctenium aegyptium*. Among the cpDNA clones used, P8 did not resolve informative or unique sites. This clone covers the inverted repeat region of the chloroplast genome, a region less likely to produce informative sites because of its highly conserved nature. Small addition-deletions were also observed. The exhaustive search evaluated 945 trees of 23 to 39 steps in length and retained a single, most parsimonious tree of 23 steps. The consistency index (CI) and retention index (RI) for the most parsimonious tree were 0.70, reflecting the relatively low homoplasy on the tree. The bootstrap and the decay index values for the different clades are given in Figure 1.

Discussion

Evolution of the *E. coracana*–*E. indica*–*E. tristachya* complex

1. Evolution of Tetraploid Species

The evolution of the tetraploid *E. coracana* subsp. *coracana* and subsp. *africana* and its genomic relationship to the diploid *E. indica* has been the focus of various studies (see introduction). This cpDNA study did not resolve restriction site differences between the two subspecies of *E. coracana*. A similar finding was also obtained in a previous cpDNA study (Hilu, 1988) that focused on the two subspecies of *E. coracana*, *E. indica*, and *E. tristachya*. These studies thus provide evidence in support of the direct origin of finger millet (*E. coracana* subsp. *coracana*) from *E. coracana* subsp. *africana*. Additional evidence in support of this theory comes from restriction fragment variation in the intergenic spacer region (IGS) between the 17S and 25S ribosomal genes (rDNA). Hilu and Johnson (1992) showed that the domesticated subspecies is quite homogeneous in IGS pattern and that its rDNA phenotype is identical to one of the IGS phenotypes detected in subspecies *africana*. In contrast, recent isozyme data (Werth et al., 1994) demonstrated the presence of alleles in domesticated finger millet, subspecies *coracana*, which were not shared with the proposed wild ancestor subspecies *africana*. Consequently, the study questioned the possibility of a direct origin of subspecies *coracana* from subspecies *africana*. This disagreement has two possible explanations. One, the two tetraploid taxa had different origins, sharing only one common diploid genome; the donor of the second genome might have contributed the unique alleles reported in subspecies *coracana*. This hypothesis is inconsistent with cytogenetical information (Chennaveeraiah & Hiremath, 1974; Hiremath & Salimath, 1992) that demonstrated complete genome homology between the two taxa. Two, the tetraploid subspecies *africana* is genetically quite variable due to high diversity incurred by polyploidization and possible multiple origin, and subspecies *coracana* was derived from a limited number of populations of subspecies *africana*, a situation typical of crops. Variability in subspecies *africana* was demonstrated in the ribosomal interspacer region (Hilu & Johnson, 1992), isozyme alleles (Werth et al., 1994), and in random amplified polymorphic DNA (RAPD) markers (Hilu, 1995). The rDNA and RAPD studies demonstrated that the DNA patterns

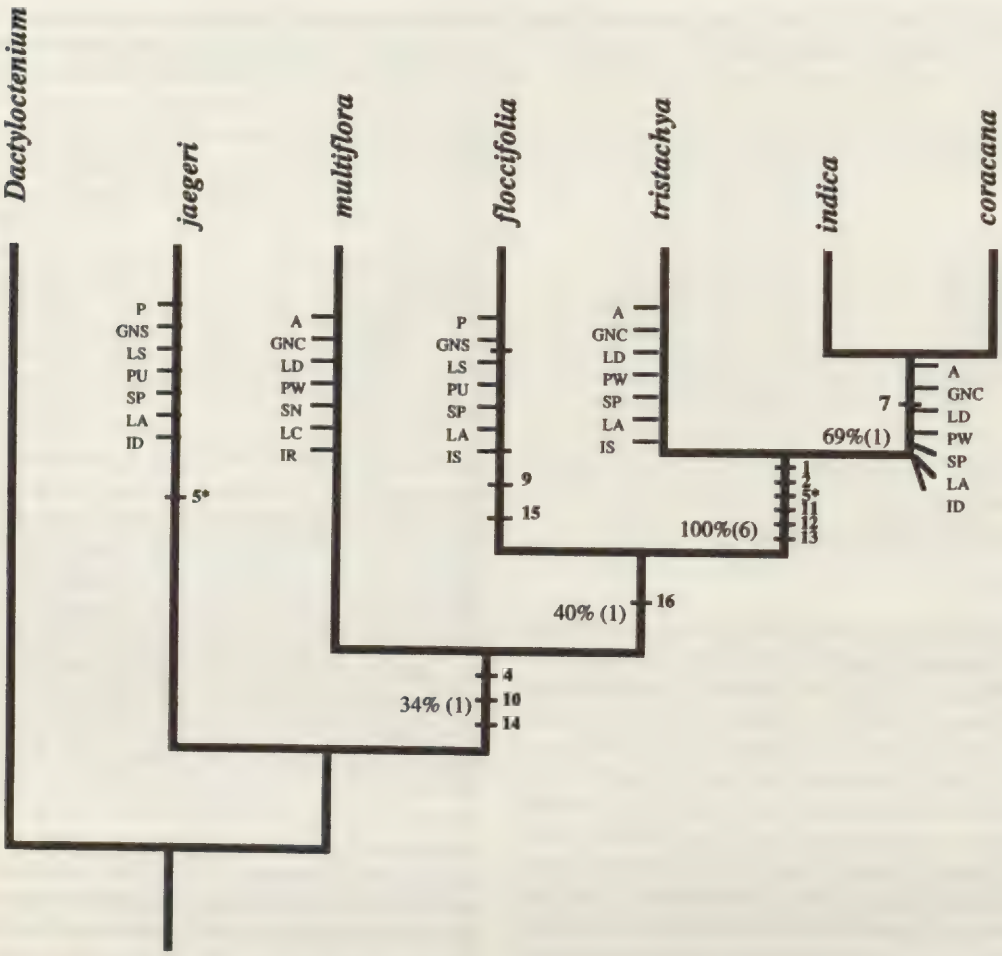

Figure 1. The single most parsimonious tree for the *Eleusine* species rooted with *Dactyloctenium aegyptium* and based on 16 phylogenetically informative cpDNA restriction sites. The two subspecies of *E. coracana* are lumped together since they are identical in restriction sites. The tree was generated through heuristic search with MULPARS, TBR branch swapping, and Simple addition. Numbers on the branches indicate unambiguous apomorphic restriction sites; homoplasy is denoted by an asterisk. Bootstrap support is indicated as percentages based on 100 bootstrap replications, while number of additional steps required to collapse each branch (decay index) is noted in parentheses. The habit and six morphological characters pertaining to the inflorescence, flower, and caryopsis are mapped on the cladogram: A, annual; P, perennial; GNS, glume nerve simple; GNC, glume nerve compound; LS, lemma simple; LC, lemma compound; LA, lemma acute; LC, lemma cuspidate; PW, palea winged; PU, palea unwinged; SP, seed surrounded by pericarp; SN, seed nacked (i.e., seed free of pericarp); ID, inflorescence digitate; IS, inflorescence subdigitate-racemose.

(phenotypes) of subspecies *coracana* are present in and can be derived from those of subspecies *africana*, and that these phenotypes represent only a subset of the genetic variation in that tetraploid wild taxon. Due to the demonstrated genetic variability in subspecies *africana*, the isozyme data might represent only part of that variation. Therefore, the origin of the domesticated taxon from one or a few genotypes of the wild tetraploid is a more likely explanation for the incomplete concordance between the isozyme data and the other molecular information. This explanation is strongly supported by the genomic homology and interfertility between the two taxa (Hiremath & Salimath, 1992). A more extensive isozyme study that includes a large sample of subspecies *africana* from across its range of distribution might shed some light on this disagreement.

Eleusine indica shares the same restriction sites with the two tetraploid subspecies of *E. coracana*, indicating the presence of a common chloroplast genome among the three. This study thus further

supports a previous cpDNA investigation (Hilu, 1988) that pointed to *E. indica* as the "A" genome donor of the tetraploid *E. coracana*. Originally, the diploid species *E. indica* was considered as the genomic donor of finger millet (Greenway, 1945; Kennedy-O'Byrne, 1957; Jameson, 1970). Based on lack of chromosome pairing in a synthetic hybrid between *E. coracana* subsp. *coracana* and *E. indica*, Chennaveeraiah and Hiremath (1974) concluded that the latter species did not contribute any of the genomes of finger millet. That study, however, was based on a single interspecific hybrid. In a more recent cytogenetic study based on more than one hybrid, Hiremath and Salimath (1992) found an appreciable amount of chromosome pairing between the *E. coracana* subsp. *coracana* and *E. indica* genomes, confirming the genomic contribution of *E. indica* to the tetraploid *E. coracana* as proposed by the cpDNA study (Hilu, 1988).

2. *Origin of E. tristachya*

To address the question of the origin and dispersal of the vicariant *Eleusine tristachya*, three points have to be considered. First, the monophyly of *E. tristachya* and *E. coracana* and *E. indica* is substantiated by information from this study (100% bootstrap, decay index of 6, and five unambiguous mutations) as well as from previous molecular, biochemical, and cytogenetic work (Hilu et al., 1978; Hilu & Johnson, 1992; Hiremath & Salimath, 1992: Werth et al., 1994). Second, all the other species of *Eleusine* are native to East Africa and are widely distributed in that region, even when they are found on other continents. Third, *E. tristachya* has relict populations in the Sudan area of Africa. Considering these points, a South American origin of *E. tristachya* is not likely. The species, at its incipient stages of differentiation from the common ancestor of the annuals (species in the terminal clade, Fig. 1), must have moved to South America during the early stages of continental drift. Clayton's (1981) study of the geographic distributions of grass genera promoted the possibility of a Tertiary spread of grass genera across the Atlantic when the latter was a relatively narrow water passage. Dispersal during the post-Columbus trading times is less likely because of the very limited distribution of *E. tristachya* in northeastern Africa.

INTRAGENERIC SYSTEMATIC RELATIONSHIPS

In her revision of the African species of *Eleusine*, Phillips (1972) asserted that the genus can be divided into two groups of species on the basis of the annual and perennial habit. She indicated that within each group, the differences between species are often small, and that among the annuals in particular, introgression is frequent. In addition to the annual and perennial habit, Phillips cited differences among the two groups of species in spikelet morphology, such as the number of nerves and the presence of a keel in the glumes and lemma, and in the presence of a keel in the palea. These morphological characters are mapped on the cpDNA cladogram (Fig. 1). On the basis of inflorescence and spikelet characters, the annual *E. multiflora* occupies an isolated position in relation to the annual species and the genus as a whole. Its racemelike inflorescence is atypical of the digitate-spike arrangement in *Eleusine*. Phillips (1972) also noted that *E. multiflora* can be distinguished from the other African species of *Eleusine* by the short, broad spikes. The lemma keel of *E. multiflora* extends into a cusp or a mucro, unlike other species of *Eleusine* where the keel does not extend at the lemma tip. The seed of *E. multiflora* ruptures from the membranous pericarp before it is dispersed from the spikelet, whereas in the other species the seed remains enclosed in the pericarp after dispersal.

The most parsimonious tree based on the cpDNA data showed the three annual species *Eleusine coracana, E. indica,* and *E. tristachya* as a terminal lineage strongly supported by six unambiguous restriction sites, a decay index of 6, and 100% bootstrap value (Fig. 1). The fourth annual species, *E. multiflora,* appeared in an individual clade situated between the two perennial taxa. Among the perennials, *E. floccifolia* emerged as a sister species to the annual species assemblage of *E. coracana, E. indica,* and *E. tristachya.* The *E. floccifolia* clade was supported by 40% bootstrap and one unambiguous restriction site mutation. The other perennial, *E. jaegeri,* formed a basal clade in the genus, diverging after the outgroup *Dactyloctenium aegyptium.* The position of the *E. floccifolia* clade as a sister taxon to the three annual species receives support from chromosome number and meiotic chromosome behavior (Chennaveeraiah & Hiremath, 1973; Hiremath & Salimath, 1992). These three annual species and *E. floccifolia* are diploids or polyploids based on $x = 9$, in contrast with the basic number of $x = 10$ for *E. jaegeri* and $x = 8$ for *E. multiflora.* Crosses between *E. floccifolia* and the annuals *E. tristachya* and *E. coracana* subsp. *coracana* revealed a good amount of genome homology, with a mean of 7.6 to 8.6 bivalents (Chennaveeraiah & Hiremath, 1973; Hiremath & Salimath, 1992). The high affinity between *E. floccifolia* and the three annual species was also demonstrated

in the isozyme study of Werth et al. (1994). The basal position of *E. jaegeri* in *Eleusine* was previously demonstrated on the basis of isozyme information (Werth et al., 1994). The chromosome numbers for the two other perennials *E. intermedia* and *E. kigeziensis* were reported to be $2n = 18$ and 38, respectively (Hiremath & Salimath, 1991). The $2n = 18$ is indicative of the diploid nature and a basic number of $x = 9$ for *E. intermedia*, a species that appears to be morphologically intermediate between the perennial *E. jaegeri* and the annual complex of *E. coracana–E. indica* (Phillips, 1972). The phylogenetic arrangement of the *Eleusine* species could point to a descending order of aneuploid chromosomal evolution from $x = 10$ to both $x = 9$ in the annual species *E. coracana*, *E. indica*, and *E. tristachya* and the perennial *E. intermedia*, and $x = 8$ in *E. multiflora*. The chromosome count of $2n = 38$ for *E. kigeziensis* needs to be verified since it appears as an aneutetraploid when compared with the basic numbers $x = 8$, 9, and 10 found in *Eleusine*. Hiremath and Salimath (1982) proposed that $x = 9$ not $x = 10$ as the primitive number in *Eleusine*, from which other basic numbers were derived.

This cpDNA study unequivocally supports the monophyly of the three annual species *Eleusine coracana*, *E. indica*, and *E. tristachya* (Fig. 1). It also substantiates the placement of the annual *E. multiflora* within the genus with three unambiguous mutations, but in a lineage distinct from the clade of the other annuals. Consequently, the results indicate that the annual condition appears to have arisen twice in *Eleusine*. The perennial species did not emerge as a monophyletic group. The internal placement of *E. multiflora* among the perennials is probably due to the exclusion from the analysis of the 10 mutations that are unique to this species. When the decay analysis was performed, the three basal clades representing the two perennials and *E. multiflora* in the most parsimonious tree collapsed into a polytomy with one additional step. Forcing *E. jaegeri* and *E. floccifolia* into a monophyletic clade with the Constraint option, the new tree was only two steps longer and the CI index slightly lower (0.64 vs. 0.70). It is to be noted that the basal branch that represents the perennial *E. jaegeri* is supported by only one, homoplasic apomorphy (Fig. 1). These analyses show low support for the basal nodes and imply a weak resolution at the base of the tree.

Further information on the systematics of *Eleusine* comes from previous biochemical, molecular, morphological, and cytogenetical studies. Hilu et al. (1978) surveyed flavonoid variation in the four annual species of *Eleusine*, the perennial *E. floccifolia*, and *Ochthochloa compressa* (Forssk.) Hilu (a taxon closely allied to *Eleusine*). Although the study could not be used to draw a conclusion concerning the perennials since only one species was represented, it highlighted the similarities among the annuals and underscored a closer affinity of *E. multiflora* to *Eleusine* than to *Ochthochloa*. *Eleusine multiflora* shared three flavonoids common to all other *Eleusine* species but lacking in *O. compressa*. The isozyme study of Werth et al. (1994) substantiated the genetic similarities among the annual species as a group and confirmed the taxonomic affinities of *E. multiflora* to *Eleusine*. Information from restriction site variation in the ribosomal intergenic spacer region (IGS) of six species of *Eleusine* revealed a similar pattern of affinities (Hilu & Johnson, 1992). The study showed the annuals, except for *E. multiflora*, to share similar IGS restriction sites. *Eleusine multiflora* had distinct IGS restriction sites, but displayed phenotypes that are found in *Eleusine*. The perennials *E. jaegeri* Pilger and *E. floccifolia* differed in restriction sites but had comparable IGS variants.

In a phenetic study based on 37 vegetative and reproductive morphological characters of *Eleusine* species and one species each of related *Dactyloctenium* and *Ochthochloa*, Hilu and deWet (1976a) showed the segregation of the annuals (except for *E. tristachya* and *E. multiflora*) in a distinct cluster linked at a correlation coefficient value of about 0.54. The two subspecies of *E. coracana* and *E. indica* formed a tight cluster. *Eleusine tristachya* formed a cluster with *Ochthochloa compressa*. All five perennial species formed one well-defined group with two subgroups; one included *E. intermedia* and *E. semisterilis*, whereas the other contained *E. floccifolia*, *E. kigeziensis*, and *E. jaegeri*. *Eleusine multiflora* formed a group with *D. aegyptium* that was last to cluster with the *Eleusine* species. Therefore, the morphological study confirms the taxonomic affinities among the perennial species and underscores the distinct position of *E. multiflora*. The spikelet morphology of the annual *E. tristachya* has possibly led to the separation of this species from the remaining annuals.

It is evident from the cpDNA and the above studies that the annual species *Eleusine coracana*, *E. indica*, and *E. tristachya* represent a monophyletic group of closely related species and that the remaining annual *E. multiflora* is a morphologically and genetically distinct taxonomic entity in the genus. The raceme-type inflorescence of this species in a predominantly digitate-type genus could raise the question of whether *E. multiflora* is a member

of *Eleusine*. The inflorescence of *E. tristachya* and some collections of *E. coracana* subsp. *africana* show a tendency toward the raceme-type (Hilu & deWet, 1976b). Removing *E. multiflora* from *Eleusine* will only create another monotypic genus, as the species would not fit well in other related genera. The taxonomic treatment of the perennial species remains problematic. None of the morphological treatments is phylogenetically based and, thus, it is difficult to compare them with the cpDNA results. Available evidence, therefore, points to a possible paraphyletic origin of these taxa from an ancestral stock of *Eleusine*, as the monophyly of the genus is well demonstrated in this investigation.

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THE FRUITS OF *JASMINUM MESNYI* (OLEACEAE), AND THE DISTINCTION BETWEEN *JASMINUM* AND *MENODORA*[1]

Jens G. Rohwer[2]

Abstract

The fruit and seed morphology and anatomy of *Jasminum mesnyi* are described here for the first time, as part of a larger comparative study on the fruit and seed structures in the Oleaceae. The evidence presented here weakens the current delimitation between *Jasminum* and *Menodora*. As usual in *Jasminum*, the two carpels of the ovary of *J. mesnyi* grow up independently to form separate mericarps, while the septum remains small. At maturity, however, the mericarps dry out and dehisce loculicidally on their adaxial side, from the style outward. The wall of the mericarps is membranous at their distal ends, but increasingly thickened toward the base. This is unique in *Jasminum* but reminiscent of *Menodora*, where the mericarps of most species show circumscissile dehiscence. The seed coat of *Jasminum mesnyi* is as unequal-sided as in *Jasminum nudiflorum*, which in turn shares dry, irregularly fragmenting mericarps with *Menodora spinescens*. After a discussion of the characters supposed to separate the two genera, it is concluded that the discontinuity between them is not greater than among some of the sections of *Jasminum*. A decision on the final status of these taxa is deferred until detailed molecular evidence becomes available.

Jasminum is by far the largest genus within the Oleaceae, although recent estimates as to its number of species differ widely, from ca. 200 (Green, 1994) to ca. 450 (Mabberley, 1987). The vast majority of the species have white flowers and opposite leaves, whereas the eight species of section *Alternifolia* DC. (Green, 1961) are characterized by yellow flowers and alternate leaves. Only two species, *Jasminum nudiflorum* Lindl. and *J. mesnyi* Hance, combine yellow flowers with opposite leaves. The fruit of *Jasminum* is usually described as a double berry, which arises through independent growth of the two carpels of the ovary, while the septum grows much in thickness but very little in extent. In earlier papers (Rohwer, 1993, 1994, 1995b) it was shown that the fleshy part of the fruit originates from the seed coat rather than the pericarp, and that the seed structure allows one to distinguish the sections of the genus. *Jasminum nudiflorum* turned out to be unusual in that its fruit does not become black at maturity but rather dries out and fragments irregularly, releasing the seeds. The fruit of the closely related *Jasminum mesnyi*, however, remained unknown, even though the species is frequently cultivated as an ornamental. Fletcher (1916) reported that "*J. primulinum* Hemsl.," as the species is usually called in the horticultural trade, had to be introduced to England as whole plants, because the plant collector E. H. Wilson, working for Veitch's nurseries, had searched in vain for seeds. Fletcher claimed that he had obtained a few seeds of *J. mesnyi* from pollination with both its own pollen and that of *J. nudiflorum*, but gave no details about the fruit. Otherwise, the species has obviously been propagated only vegetatively so far. Green (1965) commented on the apparent sterility of the cultivated plants, citing different chromosome counts ($2n$ = 24, 26, 39) and suggesting that at least some clones were triploid.

Materials and Methods

In the botanic garden of Heidelberg, attempts to achieve fruit-set in *Jasminum mesnyi* by artificial pollination (either geitonogamously, since all plants within reach were from the same clone, or with pollen from *J. nudiflorum*) failed for several years. Only after these attempts had been abandoned were four young fruits found in April 1996. One of them was fixed in FAA (5 ml formalin, 5 ml glacial acetic acid, 56 ml ethanol 96%, aqua dest. ad 100 ml) on May 24, at an obviously immature stage. The other three were bagged in nylon nets, as a precaution against loss due to premature abortion, with the hope that at least one of them would develop until maturity. The bags were inspected at intervals of

[1] I thank P. S. Green (Kew) for providing literature unavailable in Germany. S. Ball stained and mounted the sections, and U. Wagenfeld processed the photos.

[2] Institut für Spezielle Botanik, Universität Mainz, 55099 Mainz, Germany.

two to three days. The fruits slowly became larger and paler, but did not look quite mature even on June 17. On June 19 they were found open, with the seeds still attached in one of them but shed into the bag in the others. All available material was fixed in FAA. A flowering voucher specimen (*Rohwer 135*) of the investigated plant had been deposited in HEID earlier.

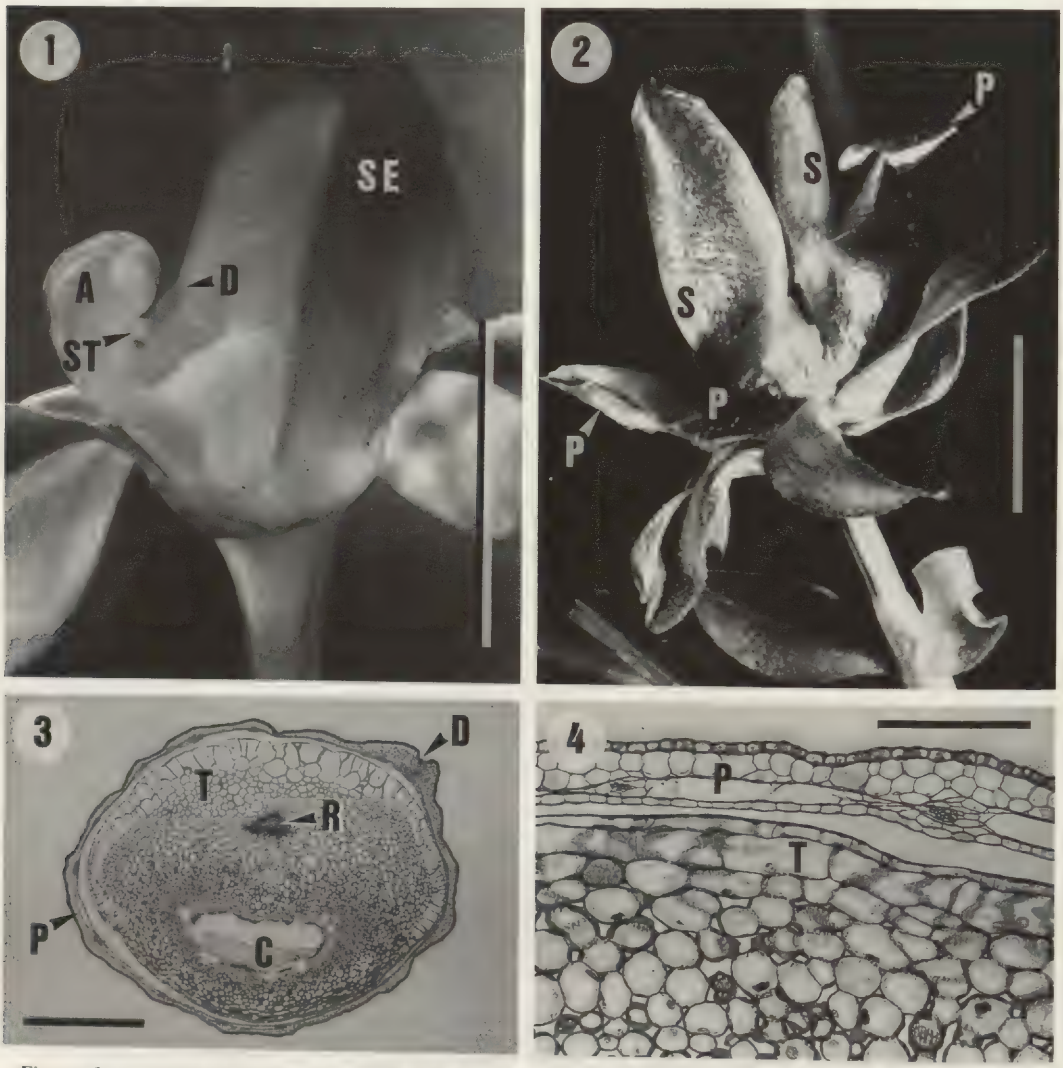
For sectioning, the material was transferred to 70% ethanol for at least a day, then embedded in a 2-hydroxy-ethyl methacrylate resin (Kulzer's Technovit 7100; for details, see Igersheim, 1993), sectioned with a rotary microtome (Leica RM 2145) at a thickness of 3–6 μm, stained with Giemsa solution for 2 hr. (2.5 ml Gurr's improved R66 in 100 ml aqua dest.), differentiated in aqua dest. with two or three drops of acetic acid and subsequently in 96% ethanol, each for about 5–20 sec. according to the intensity of the stain, transferred to xylene via isopropanol, and enclosed in Vitro-Clud embedding medium. The microphotos were taken with a Zeiss Axioskop on Agfapan APX 25 film.

Results

In the young fruit of *Jasminum mesnyi* (Fig. 1), it is obvious that both carpels of the ovary had started to grow up to form separate mericarps. In all four fruits, however, one of the two mericarps ended its development early, while the other continued to grow. In this case the developing mericarp shifts to a position almost in continuation of the pedicel, displacing the aborted mericarp and the remnant of the style sideways. Early on, a longitudinal ridge with a shallow furrow in its middle becomes visible close to the style (Fig. 1), becoming more and more distinct and stretching more toward the distal end of the developing mericarp with maturity. At maturity, not only the fertile mericarp but the whole fruit opens along this suture, splitting the style in half (Fig. 2). In one of the three mature fruits the dehiscence continued in a straight line along the carpel median, over the tip down to the base of the fertile mericarp. In the other two the splitting was straight only slightly beyond the point where the suture becomes indistinct, followed by an irregular, branched crack above.

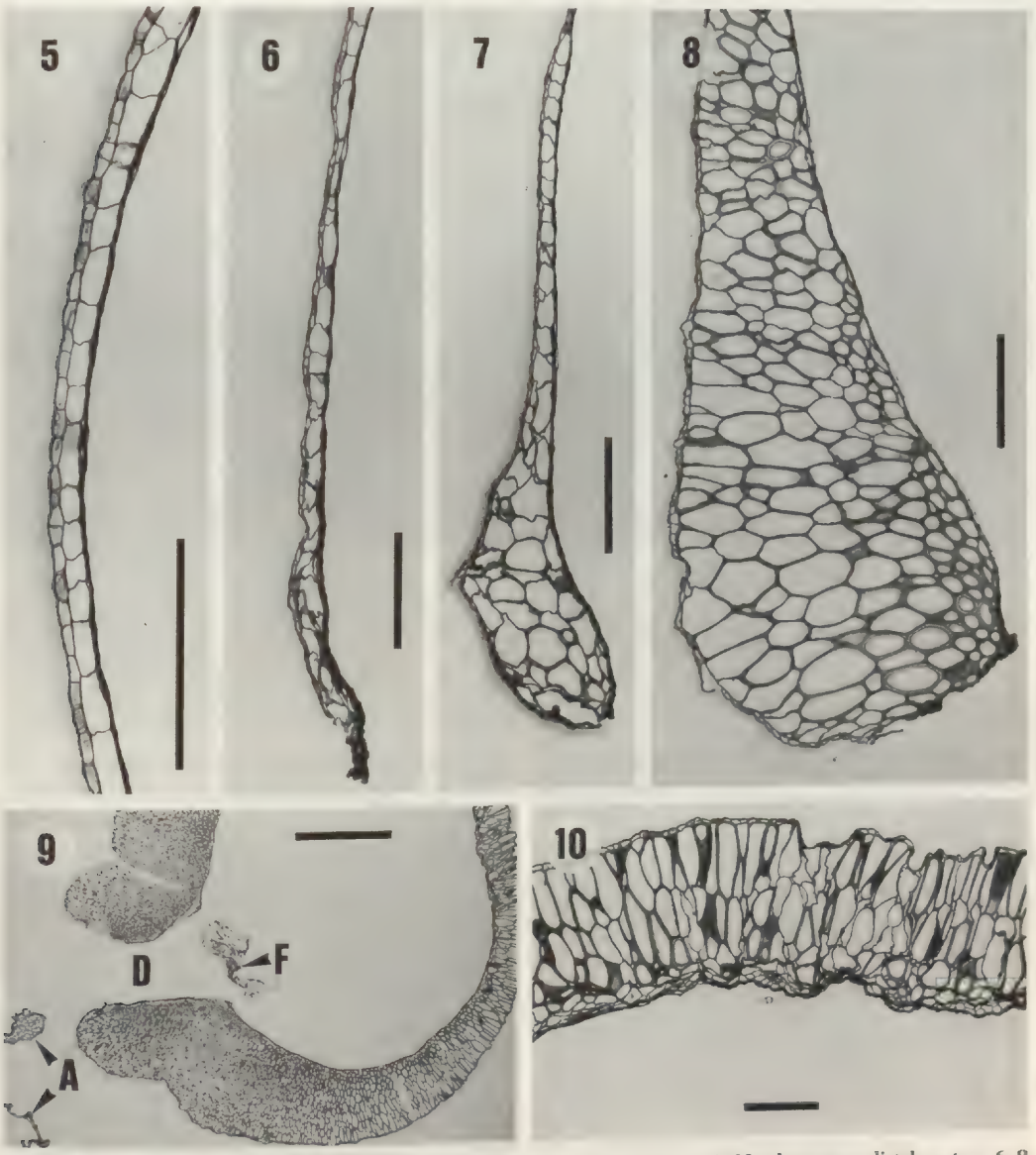
In the immature fruit (Figs. 3, 4), the pericarp consists of an outer epidermis of small, isodiametric to slightly flattened cells with a rather thick cuticle, several at least initially parenchymatous layers, and an inner epidermis of small, thin-walled, slightly flattened cells. Numerous small, weakly developed vascular bundles are found embedded among the inner parenchymatous layers. These layers, about four to six in the distal part of the mericarp, cannot keep up with the growth of the fruit in the areas between the vascular bundles, so that they are destroyed early in fruit development. The outer epidermis, some outer parenchymatous layers (one or two distally, more toward the base), and the inner epidermis remain distinct for most of the fruit development. At maturity, only the outer epidermis and its hypodermal layer are still recognizable in the distal part of the mericarp (Figs. 5, 6). Slightly below the tip, the fruit wall becomes thicker on both sides of the dehiscence line, and polygonal cells with slightly thickened, pitted, lignified walls appear (Fig. 7). The most distal ones of them are more or less isolated, but soon they aggregate to form woody strands along the suture. Further toward the base, these strands not only become thicker but also extend further around the mericarp (Fig. 8). Even at the base, however, there are about as many parenchymatous as sclerified cells in the abaxial wall of the mericarp (Figs. 9, 10). The outer and the inner epidermis, the (usually no more recognizable) inner parenchymatous layers, and several layers forming the weakness zone within the suture are never lignified. Otherwise, the thickness of the cell walls and the degree of lignification increase from the abaxial side of the mericarp toward the suture, and from the outside inward.

The seeds are elongate, about 8–10 mm long and 3.5–4.5 mm wide. Their outline in cross section (Fig. 11) is thickly plano-convex when both ovules of a locule develop; otherwise it is elliptic. The two seeds face each other with their raphal sides. The seed coat consists of numerous cell layers, of which the inner ones are gradually destroyed by the growing endosperm. As in other species of *Jasminum*, but in contrast to most other Oleaceae, there is no trace of an endothelium (jacket layer) at any time during development. The two outermost layers are very different from the rest of the seed coat, and unequally developed on the two sides of the seed (Figs. 11, 12). On the antiraphal side (Fig. 13), the outer epidermis (exotesta) consists of small, transversely elongate cells with thickened, lignified walls, more massive on the outside than on the inside. The cells of the hypodermal layer are much larger, with massive, lignified thickenings occupying almost their entire anticlinal walls, and much smaller thickenings on the periclinal walls. All further layers are parenchymatous and entirely collapsed at maturity. On the raphal side (Fig. 14), the cells of the exotesta are much larger,



Figures 1–4. Fruits of *Jasminum mesnyi*. —1. Immature fruit, the sepal in front removed. —2. Mature, open fruit with the seeds (S) still attached. —3. Cross section of young fruit, approximately at the middle. —4. Cross section of young pericarp and outer layers of young testa. A = aborted carpel, C = cotyledons, D = dehiscence line, P = pericarp, R = raphe bundle, S = seed, SE = sepal, ST = style, T = immature testa. Scale bars in 1, 2 = 5 mm, in 3 = 1 mm, in 4 = 200 μm.

forming a palisade of hexagonal cells. The lignified wall thickenings are much weaker and almost entirely restricted to the anticlinal walls, usually to the corner where three cells meet. The cells of the hypodermal layer are longitudinally elongate and smaller than those of the exotesta, though still larger than on the antiraphal side. They have (mostly two) band-shaped wall-thickenings in their anticlinal walls, occasionally also in their outer periclinal wall. When the seed dries out, the two outer layers separate from the rest of the seed coat, tearing apart the thin inner end of the anticlinal cell walls in the hypodermal layer. In the area where this separation occurs, several of the following cell layers have band-shaped wall thickenings as well, much smaller than in the hypodermal layer and becoming still smaller and more irregularly distributed toward the inside (Fig. 14). Below them follows the raphal bundle, which is the only vascular bundle of the seed, and several parenchymatous layers that are increasingly collapsed toward the inside. About three to five (only apically and basally more) layers of endosperm surround the embryo, which has very large, flat cotyledons with well-developed, usually two-layered palisade paren-

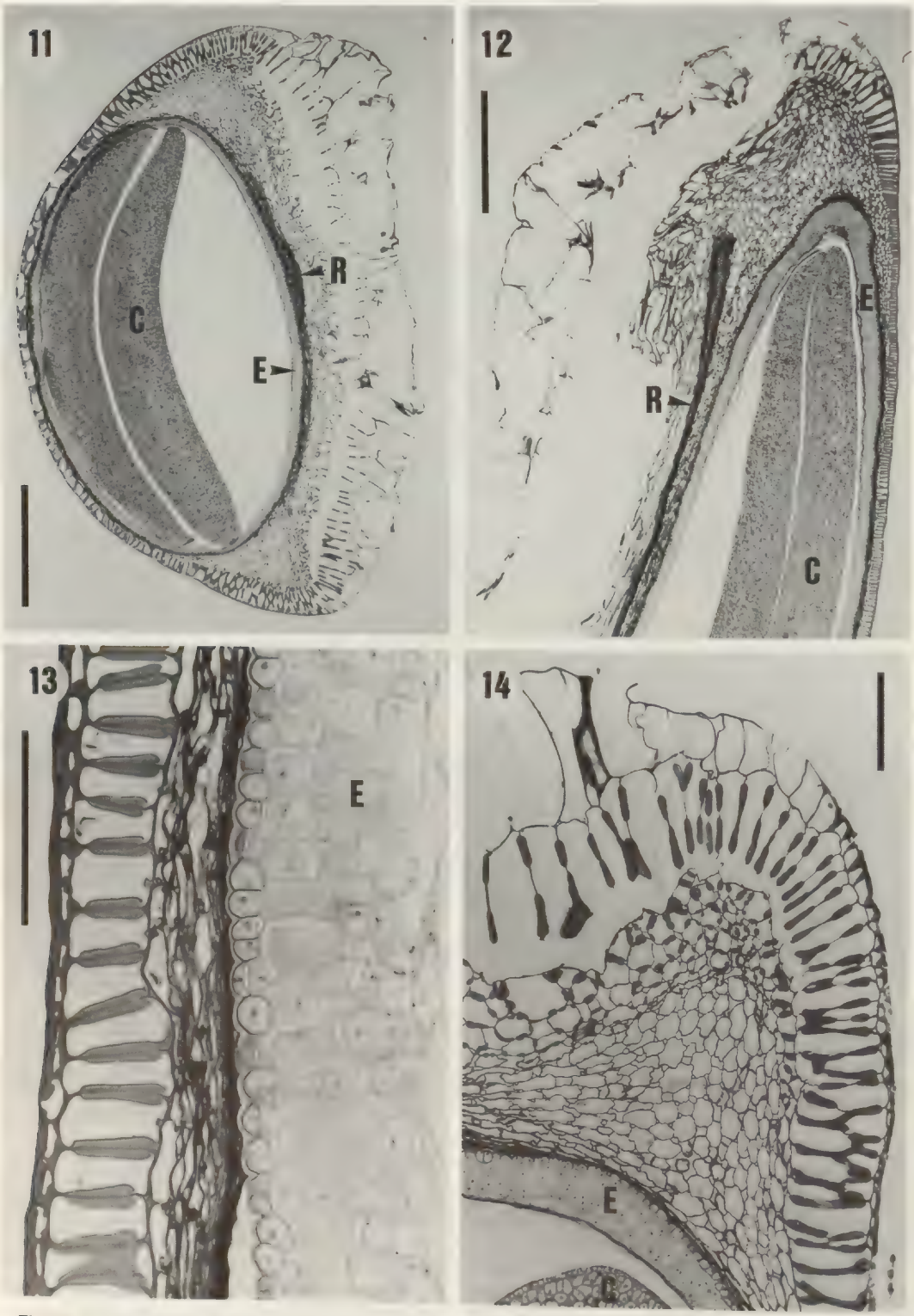


Figures 5–10. Cross sections of mature pericarp of *Jasminum mesnyi*. —5. Membraneous, distal part. —6–8. Pericarp with dehiscence line (bottom), from slightly below the apex of the mericarp (Fig. 6) to slightly below the middle (Fig. 8). —9. Basal part of the fertile mericarp, slightly above the level where the two mericarps become separate. —10. Pericarp on abaxial side, same section as in Figure 9. A = remains of aborted carpel, D = dehiscence line, F = remains of funicular tissue. Scale bars in 5, 6, 7, 8, 10 = 200 μm, in 9 = 1 mm.

chyma. Starch was not found in either the endosperm or the embryo.

Discussion

The fruit of *Jasminum mesnyi* agrees with that of the other species of *Jasminum* in the development of two separate mericarps. With its loculicidal dehiscence, however, it goes beyond the current circumscription of the genus, which has normally indehiscent fruits with a membranous to coriaceous pericarp and seeds with a fleshy testa. Dry but irregularly fragmenting fruits, and seeds with an almost identical structure as in *J. mesnyi*, have recently been described in another well-known ornamental species, *J. nudiflorum* (Rohwer, 1993, 1994, 1996). The development of a median suture can even be observed in young fruits of this species (Fig. 15), but none of the open fruits observed so far had actually dehisced along this line. In addition, the pericarp of *J. nudiflorum* is almost ho-



Figures 11–14. Seeds of *Jasminum mesnyi*. —11. Cross section. —12. Longitudinal section, chalazal end. —13. Testa and endosperm on antiraphal side, longitudinal section. —14. Edge of raphal side (above), cross section. C = cotyledon, E = endosperm, R = raphe bundle. Scale bars in 11, 12 = 1 mm, in 13 = 100 μm, in 14 = 200 μm.

Figures 15, 16. Comparable fruit structures in other species. —15. *Jasminun nudiflorum*, very young stage of fruit development. —16. *Menodora africana*, mature fruit, the mericarp on the left open and empty, the one on the right still closed, showing the difference between the thicker proximal part and the thinner distal part (hexagonal wall thickenings of the seed coat shining through). A = Aborted mericarp, D? = ridge with longitudinal furrow, similar to the dehiscence line in *J. mesnyi*. Scale bars in 15 = 1 mm, in 16 = 5 mm.

mogeneously membranous throughout, with only a few stone cells near the base, so that it lacks the mechanism for an orderly dehiscence. All other characters, however, whether vegetative, floral, or seed characters, show beyond doubt that the two species are very closely related. Still the differences appear important enough to reject the view expressed by Henry (1904), who thought that "*J. primulinum*" was just a variety of *J. nudiflorum*.

Fruits with dry, dehiscent mericarps are, within the Oleaceae, the most important diagnostic character for *Menodora*, a small genus (22 spp.; Steyermark, 1932; Turner, 1991, 1995) of low shrubs or, more frequently, suffruticose to almost entirely herbaceous plants. In this genus, however, the dehiscence of the fruits is not longitudinally loculicidal but normally circumscissile (Fig. 16). In *M. africana* Hook. at least, where the fruits and seeds have been described in detail recently (Rohwer, 1995a), the pericarp is thicker below the equatorial suture line, but does not contain stone cells, or any other lignified elements, except in the very base of the fruit. No trace of a median suture line was found in this species, at any stage of development.

As an exception within the genus, Steyermark (1932) described the presence of a median suture in *Menodora spinescens* A. Gray, but he never found fruits that had opened along this line. The shape of the fruit is likewise unusual. The mericarps are elongate and spreading in *M. spinescens*, whereas they are subglobose and more or less appressed against each other in the other species. *Jasminum mesnyi* has similarly elongate mericarps, and this suggests that they would most likely spread if both were developed. In *J. nudiflorum*, in contrast, they are roundish and adjoining. This character seems to be of minor significance, since there are many parallel cases and intermediate forms known from *Jasminum*, often in closely related species (e.g., roundish/adjoining in *J. bignoniaceum* Wall. ex G. Don, intermediate in *J. humile* L., elongate/spreading in *J. odoratissimum* L.). More important is the aberrant number of ovules in *M. spinescens*. While the other species of *Menodora* have four ovules per locule, *M. spinescens* has only two, like most other Oleaceae, including the yellow-flowering species of *Jasminum*, whereas the majority of the white-flowering species of *Jasminum* have only one. This again bridges the discontinuity between the two genera. In *Menodora*, the information given by Steyermark (1932) and Turner (1991) suggests that *M. spinescens* is the only species with basically white flowers (often tinged with brownish purple), whereas the basic flower color of the other species is yellow (sometimes tinged with red to purple).

Inasmuch as the fruits of *Jasminum mesnyi* and *Menodora spinescens* suffice to undermine the traditional distinction between *Jasminum* and *Menodora*, it may be worthwile to examine other characters that could possibly separate the two genera (summarized in Table 1). Habit (shrubs and climbers in *Jasminum* versus at most subshrubs in *Men-*

Table 1. Distinguishing features of selected taxa of *Jasminum* and *Menodora*.

	Jasminum sect. *Jasminum*	*Jasminum* sects *Tri- & Unifoliolata*	*Jasminum* sect. *Alternifolia*	*Jasminum nudiflorum*	*Jasminum mesnyi*	*Menodora spinescens*	*Menodora africana*	Most *Menodora* spp.
Habit	climbers	shrubs/climbers[a]	shrubs	shrubs	shrubs	shrubs	herbs	±herbs[b]
Leaf arrangement	opposite	opposite	alternate	opposite	opposite	alternate	opp. or alt.	opposite
Leaves	pinnate	trifol./simple	trifol. or pinn.	trifoliate	trifoliate	simple	dissected	simple
Flower color	white	white	yellow	yellow	yellow	whitish	yellow	yellow
Corolla tube/anthers	long/included	long/included	long/included	long/included	long/included	short/exserted	short/exserted	short/exserted[c]
Ovules per locule	usually 2	usually 1	2	2	2	2	4	4
Fruit at maturity	fleshy, black	fleshy, black	fleshy, black	pale, dry	pale, dry	pale, dry	pale, dry	pale, dry
Shape of mericarps	variable	variable	variable	roundish	elongate	elongate	roundish	roundish
Dehiscence of mericarps	—	—	—	irregular	longitudinal	irregular	circumscissile	circumscissile
Median suture	—	—	—	rudimentary	functional	non-functional	—	—
Vascular bundles/seed	1	many	1	1	1	1	1	unknown
Structure of exotesta	sarcotesta	sarcotesta	small-celled	unequal[d]	unequal[d]	not preserved	small, thickened	unknown
Gap within testa	—	—	—	+	+	+	+	unknown
Mesotestal layers with wall thickenings	1	several	several	unequal[e]	unequal[e]	3	3	unknown
Cotyledons	flat or storage	storage	flat	flat	flat	flat	flat	probably flat
Chromosome number 2*n*	26	26	26	52	24, 26, 39	unknown	unknown	22[f]

[a] *Jasminum siamense* is only suffrutescent.
[b] *Menodora robusta* is a robust shrub.
[c] But *Menodora longiflora*, in all other characters a typical *Menodora*, has a long corolla tube with included anthers.
[d] Small, thick-walled cells on antiraphal side, sarcotesta on raphal side.
[e] One on antiraphal side, several on raphal side.
[f] So far only North American species examined.

odora) is rarely used as a diagnostic character (or only as a supplementary character, as by Verdoorn, 1956, 1963), but is frequently mentioned in descriptions. However, *M. robusta* (Benth.) A. Gray and *M. spinescens* are quite robust, erect shrubs, whereas *J. parkeri* Dunn is a prostrate to decumbent shrublet and *J. siamense* Craib is (always?) a weak subshrub, both species not more than 30 cm tall. More frequently used as a diagnostic character is the relative length of the corolla tube and the position of the anthers (e.g., Kupicha, 1983). Corolla tubes that are about as long as the corolla lobes or longer, with included anthers, are characteristic of *Jasminum*, whereas exserted anthers and corolla tubes much shorter than the lobes are supposed to characterize *Menodora*. This character fails, however, in *M. longiflora* (Engelm.) A. Gray, a North American species, which has long corolla tubes and included anthers, but otherwise is typical of *Menodora*. Taylor (1945) and Johnson (1957) use chromosome number ($n = 11$ in *Menodora* vs. $n = 13$ in *Jasminum*) as a supplementary character in the diagnosis of the genera. However, it cannot yet be accepted as proven that this is a real discontinuity. While *Jasminum* appears to have been adequately sampled by now, with counts of $n = 13$ from numerous species belonging to different sections of the genus and coming from different regions of the world, the same cannot be said about *Menodora*. To my knowledge, neither the aberrant *M. spinescens* nor any South American or South African species has been examined so far.

The seed structure of *Jasminum mesnyi* and *J. nudiflorum* differs from that of all other species of both *Jasminum* and *Menodora* so far investigated. In the other species of *Jasminum*, the seeds may be plano-convex in cross section when there are two per locule, but they are never even nearly as unequal-sided as in *J. mesnyi* and *J. nudiflorum*. Our knowledge about seed structure in *Menodora* is still inadequate. Only two species have been examined so far (Rohwer, 1995a), *M. spinescens* and *M. africana*, only the latter in all stages of development. This species has an exotesta of small cells, in which the outer wall becomes so much thickened as to occlude the lumen (almost) completely, even more than on the antiraphal side in *J. mesnyi*. As a consequence of this thickening, which occurs long before maturity in *M. africana*, the exotestal cells can neither enlarge nor divide any further as the seed grows, so that the exotesta becomes discontinuous at maturity. The following layers are similar to those near the edges of the seed in *J. mesnyi*. The hypodermal layer consists of very large cells with conspicuous thickenings in the anticlinal walls, followed by a few layers of much smaller cells with much smaller, more irregularly distributed thickenings. A gap between the outer two layers and the rest of the seed coat, as on the raphal side in *J. mesnyi*, can even be observed in *M. africana*, all around the seed but more distinct on the antiraphal side. In *M. spinescens*, however, the separation occurs deeper in the seed coat, between the outer layers with thickenings and the inner parenchymatous part. The fate of the exotesta, unfortunately, could not be followed in the relatively poor material available of this species. In any case, the seed of *M. spinescens* appears more similar to that of *M. africana* than to those of any species of *Jasminum*.

In summary, the distinction between *Jasminum* and *Menodora* is not as straightforward as most treatments of the family imply, and the gap is further closed by the data presented here for *J. mesnyi*. Kim and Jansen (1993) found that *Jasminum* and *Menodora* share a 21 kb inversion in the chloroplast genome, and that *Menodora* and some species of *Jasminum* agree in the loss of *clp*A gene introns. This would suggest that *Jasminum* may be paraphyletic with respect to *Menodora*. Unfortunately, their results were published as an abstract only, so that a full comparison with their data is still impossible. A similar conclusion was reached, however, through a detailed study of the fruit and seed structures of the Oleaceae (Rohwer, 1996). With the addition of *J. mesnyi*, it becomes clear that the discontinuity between *Jasminum* and *Menodora* is not greater than the gaps encountered within *Jasminum*, namely among the species with (a) alternate leaves and yellow flowers (sect. *Alternifolia*), (b) opposite leaves and yellow flowers (*J. mesnyi* and *J. nudiflorum*), and (c) opposite leaves and white flowers (sects. *Jasminum*, *Trifoliolata*, and *Unifoliolata*). Demoting *Menodora* to the rank of a section under *Jasminum* would perhaps make the system of the Oleaceae slightly more natural, but this small gain is overcompensated by the danger of losing information on the few species of *Menodora* among the hundreds of *Jasminum*. The most logical alternative solution, i.e., giving generic rank to all four groups, should wait until the details of the molecular analysis become available; it would also require new generic names for groups a and b.

For the morphological interpretation of the relationships within the *Jasminum–Menodora* complex, it would be most important to know whether the dehiscent fruits of *J. mesnyi* were a primitive or an advanced feature. Loculicidal dehiscence as such is certainly plesiomorphic within the Oleaceae (Rohwer, 1996), but it is questionable whether this

is true also for *J. mesnyi*. On the one hand it appears unlikely that such a functional character should be at first lost and then secondarily regained within a family, but on the other hand the construction of the mechanical tissue in *J. mesnyi* is entirely different from that in the other Oleaceae. In these we find a sharply delimited endocarp, consisting of fibers that are stretched transversally to diagonally on the flanks of the fruit, but longitudinally along the suture. This pleads clearly in favor of an independent origin. It is tempting to add that it would be difficult to understand how and why three different modes of dehiscence, loculicidal, irregular, and circumscissile, would have evolved within in the *Jasminum–Menodora* complex when one of them had already been established. This, however, is a weak argument, because the presence of a nonfunctional suture in the species with irregular dehiscence (*J. nudiflorum, M. spinescens*) shows that such a development must have occurred anyway.

Considering the morphological differences within *Menodora* and the widely disjunct distribution of the genus (southwestern North America, southern South America, and South Africa), it may be asked whether *Menodora* is even monophyletic. For the bulk of the genus, there is little doubt. The combination of herbaceous habit, four ovules per locule, and separate, circumscissile mericarps is too unusual to have arisen more than once. *Menodora spinescens,* however, shows none of these character states, so that its placement within this genus (e.g., as opposed to *Jasminum*) may appear questionable. However, its minute leaves, short corolla tube, exserted anthers, and separate, dry mericarps sharply distinguish it from *Jasminum,* and make it far more similar to the typical *Menodora* species than to any other taxon. In its habit it resembles the more robust species of this genus, especially *M. robusta.* Therefore, it makes little sense to remove *M. spinescens* from the genus, unless it can be shown that it is not the closest sister group to the remaining species. Further studies are needed to elucidate its relationships within this complex.

The unexpected morphological and anatomical data presented here, in a supposedly well-known species, thus raise a number of questions that presently cannot be answered with confidence. The purpose of the present paper is to bring them to notice, for consideration in future studies.

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REVISIÓN DEL GÉNERO *GALIANTHE* SUBG. *EBELIA* STAT. NOV. (RUBIACEAE: SPERMACOCEAE)[1]

Elsa L. Cabral[2] *y Nélida M. Bacigalupo*[3]

Resumen

Se subordina al género *Galianthe* (Rubiaceae: Spermacoceae) el subgénero *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, que agrupa las especies que presentan frutos de mericarpos indehiscentes. Se reconocen nueve especies: *Galianthe bogotensis* (Kunth) E. L. Cabral & Bacigalupo, *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo, *Galianthe cymosa* (Cham.) E. L. Cabral & Bacigalupo, *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, *Galianthe dichotoma* (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo, *Galianthe hispidula* (A. Rich. ex DC.) E. L. Cabral & Bacigalupo, *Galianthe polygonoides* sp. nov., *G. humilis* sp. nov. y *G. vaginata* sp. nov.; las tres últimas viven en Brasil. Todas se describen e ilustran.

Abstract

A new subgenus, *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, is proposed within the genus *Galianthe* (Rubiaceae: Spermacoceae). The species included therein are characterized by their fruits with indehiscent mericarps. Nine species are recognized: *Galianthe bogotensis* (Kunth) E. L. Cabral & Bacigalupo, *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo, *Galianthe cymosa* (Cham.) E. L. Cabral & Bacigalupo, *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, *Galianthe dichotoma* (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo, *Galianthe hispidula* (A. Rich. ex DC.) E. L. Cabral & Bacigalupo, *Galianthe polygonoides* sp. nov., *G. humilis* sp. nov., and *G. vaginata* sp. nov.; the last three are found in Brazil. All the species are described and illustrated.

La delimitación de algunos géneros de la tribu Spermacoceae (Rubiaceae) ha planteado dificultades que se manifiestan en el distinto criterio de los autores sobre este tema.

Schumann (1891) reconoció en esta tribu 18 géneros, 13 de los cuales estaban representados en América. Posteriormente a esta lista se sumaron nuevos géneros de 1 ó 2 especies: *Diacrodon* Sprague, *Diodella* (Torr. & A. Gray) Small, *Microsepalum* Urb., *Tortuella* Urb., *Spermacoceodes* Kuntze, *Tobagoa* Urb., que no han sido totalmente aceptados. Sin embargo la mayoría de los autores en estudios florísticos regionales han seguido en término generales el criterio de Schumann, introduciendo sólo cambios menores. Verdcourt (1975: 301) señaló la dificultad en reconocer ciertos géneros casi únicamente por la dehiscencia de los frutos, sobre todo ante material florífero y además por el escaso valor que él le asigna a este carácter unitario. Este autor amplía los límites de *Spermacoce* L. y subordina a éste las especies de *Borreria* G. Mey. y *Diodia* L., si bien resalta que *Diodia virginiana* L., especie americana y tipo del género, tiene frutos de estructura diferente a las especies de *Diodia* del área africana. Verdcourt (1975) señaló que Steyermark (en litt.) concordó en gran parte con su opinión, pero a pesar de ello reconoció a estos tres géneros separadamente, ya que admitió que se podían diferenciar bien, evitando de este modo numerosos cambios nomenclaturales. En el tratamiento de las Rubiáceas de Venezuela, Steyermark (1974) mantuvo este criterio. Actualmente algunos autores se inclinan por apoyar con variantes el criterio de Verdcourt, así Chaw y Sivarajan (1989), Fosberg et al. (1981), Howard (1989) y Bur-

[1] Esta comunicación constituye una parte del trabajo Delimitation of the American Genera of the Tribe Spermacoceae (Rubiaceae) presentado durante la International Conference on the Systematics of the Rubiaceae (1993), St. Louis, Missouri. Se agradece a Angel Cabrera que realizó las diagnosis latinas y a los curadores de los herbarios de Brasil (MBM, PACA, R, RB, SP, SPF), Estados Unidos (F, MO, NY, US) y Argentina (BA, BAB, CTES, LP, SI) que nos facilitaron sus colecciones.

[2] Facultad de Ciencias Exactas, Físicas y Naturales y Agrimensura (UNNE)–IBONE, C.C. 209, 3400 Corrientes, Argentina.

[3] Instituto de Botánica Darwinion–C.C. 22, 1642 San Isidro, Buenos Aires, Argentina.

Tabla 1. Caracteres del *Ebelia* subg. *Ebelia* y del subg. *Galianthe*.

Subg. *Galianthe*	Subg. *Ebelia*
Fruto de mericarpos dehiscentes	Fruto de mericarpos indehiscentes
Flores siempre heterostilas	Flores casi siempre heterostilas, excepto en *G. dichotoma*
Semillas a veces complanadas, con bordes aliformes	Semillas nunca complanadas
Hábito erecto, con frecuencia xilopodio muy desarrollado	Hábito variado, erecto, postrado, trepador
Tallo nunca alado	Tallo casi siempre alado
Cromosomas $x = 8$	Cromosomas $x = 14, 15$
Cerca de 40 sp., América del Sur	9 sp., Centro y Sudamérica
10°–35°S	20°N–35°S

ger y Taylor (1993) reconocieron *Diodia* y *Spermacoce* y subordinaron en este género las especies de *Borreria*.

De ahí que un estudio global de los géneros de Spermacoceae analizando el mayor número de caracteres de las especies que los representan, es necesario para fundamentar los límites y las relaciones de los mismos. Con este fin se ha continuado con el estudio de los géneros *Diodia* y *Borreria*. De estos se han separado algunas pocas especies que por sus caracteres se han asimilado al género *Galianthe* (Cabral, 1991; Pire & Cabral, 1992), pero del que se diferencian por los frutos de mericarpos indehiscentes. Por esto se propone ampliar los límites del mismo e incluir las especies estudiadas en un nuevo subgénero: *Galianthe* subg. nov. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo.

Materiales y Métodos

Este estudio se ha realizado con material de los herbarios nacionales y extranjeros cuyas siglas se registran de acuerdo con Holmgren et al. (1990) (BA, BAB, BR, CTES, F, HAS, ICN, G, K, LIL, LP, MBM, MNES, MO, NY, P, PACA, R, RB, SI, SP, SPF, US).

Tratamiento Taxonómico

En el estudio emprendido de las especies americanas de los géneros *Spermacoce, Borreria* y *Diodia* se han separado unas especies que no reunen los caracteres de estos géneros: *Borreria dichasia* Sucre & C. G. Costa; *Diodia brasiliensis* Spreng., *D. brasiliensis* var. *angulata* (Benth.) K. Schum., *D. cymosa* Cham., *D. dichotoma* (Willd. ex Roem. & Schult.) K. Schum. y *D. hispidula* A. Rich. ex DC.; y *Spermacoce bogotensis* Kunth.

De esta lista, *Diodia dichotoma* fue descrita erróneamente en el género *Knoxia* L., ya que este género es considerado actualmente en una tribu independiente, Knoxieae, que se caracteriza por presentar flores con óvulos de placentación apical, péndulos, de micrópila súpera. Este error fue enmendado y la especie fue reubicada sucesivamente en los géneros *Spermacoce, Borreria,* y *Triodon* DC. por distintos autores y finalmente como *Diodia dichotoma* (Schumann, 1889).

Borreria dichasia fue descripta como *Borreria* a pesar de no haber contado con material con frutos. *Diodia cymosa* y *D. hispidula* fueron descritas dentro del género *Diodia* por sus frutos de mericarpos indehiscentes. *Spermacoce bogotensis* fue reubicada en el género *Diodia* o *Borreria* por distintos autores.

Diodia brasiliensis Spreng. fue separada por De Candolle (1830) junto con *D. anthospermoides* Cham. & Schltdl. y *D. polymorpha* Cham. & Schltdl., en un nuevo género, *Triodon*. Este autor caracterizó a dicho género por el hábito sufruticoso, las inflorescencias en fascículos espigados y los frutos de mericarpos indehiscentes y lo nominó haciendo alusión a los tres diminutos dientecitos, correspondientes a restos de hacecillos vasculares, persistentes en el ápice de los pedicelos al caer los frutos. Posteriormente Bentham agregó dos nuevas especies, *Triodon angulatum* de México y *T. laxum* de Ecuador. Este género no fue aceptado por algunos autores (Schumann, 1888; Standley, 1930; Steyermark, 1974) y posteriormente sus especies se reconocieron dentro del género *Diodia*, como uno, dos ó tres taxones distintos, por tener frutos de mericarpos indehiscentes. De Candolle al describir *Triodon* no registró el dimorfismo floral, a pesar de que incluyó como basónimo de *T. polymorphus* a *Diodia polymorpha* Cham. & Schltdl. En esta especie sus autores diferencian variedades y dan una descripción detallada de las flores brevistilas y longistilas que tienen, si bien no usan estos términos. Schumann (1889) consideró a las tres especies citadas por De Candolle, sinónimos de *Diodia polymorpha*, a pesar de que registró a una especie anterior *D. brasiliensis* Spreng. (1825) entre sus sinónimos.

El grupo de especies aquí estudiado se corresponde con los caracteres del género *Triodon*, pero este nombre genérico está invalidado por un homónimo anterior (Tabla 1) y en su lugar debe usarse *Ebelia*

Rchb. Pero *Ebelia* es muy similar a *Galianthe* Griseb., género rehabilitado recientemente (Cabral, 1991; Pire & Cabral, 1992). Ambos presentan inflorescencias amplias de ramificación cimosa, flores dimorfas y difieren por los frutos, de mericarpos dehiscentes en *Galianthe* e indehiscentes en *Ebelia*. Por lo tanto se propone ampliar los términos de la definición de *Galianthe* y subordinar *Ebelia* como: *Galianthe* Griseb. subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo.

En este nuevo subgénero se incluyen los siete taxones mencionados y tres especies nuevas de la flora brasileña: *Galianthe humilis* E. L. Cabral & Bacigalupo, *Galianthe polygonoides* E. L. Cabral & Bacigalupo y *Galianthe vaginata* E. L. Cabral & Bacigalupo.

Galianthe Griseb., Abh. Königl. Ges. Wissensch. Göttingen 24: 157. 1879. *Borreria* G. Mey. sección *Galianthe* (Griseb.) K. Schum., en Martius, Fl. Brasil. 6(6): 40–42. 1888. *Borreria* G. Mey. subg. *Galianthe* (Griseb.) Standl., Field Mus. Hist. Bot. Ser. 8 (5): 392. 1981. TIPO: *Galianthe fastigiata* Griseb.

Se amplian los límites de *Galianthe* y se reconocen dos subgéneros sobre la base de la diferencia de dehiscencia de los frutos:

1a. Frutos de mericarpos dehiscentes .. subg. *Galianthe*
1b. Frutos de mericarpos indehiscentes .... subg. *Ebelia*

Galianthe Griseb. subg. **Ebelia** (Rchb.) E. L. Cabral & Bacigalupo, comb. et stat. nov. *Ebelia* Rchb., Deut. Bot. Herb. Buch. 74. 1841. *Triodon* DC., Prodr. 4: 566. 1830, non Baumg. (1816). TIPO: *Triodon polymorphus* DC. [= *Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo] (lectótipo, aquí designado).

Hierbas perennes, sufrútices o pequeños arbustos, erectos, trepadores o postrados. Tallos tetrágonos, en general alados. Hojas con la nervadura marcada o apenas visible. Vaina estipular fimbriada, breve, rara vez tubulosa, prolongada por encima de la inserción del par de hojas correspondiente. Inflorescencias complejas, tirsoides o cimoidales, inflorescencias parciales en dicasios más o menos congestos, en fascículos o cabezuelas subglomeriformes, rara vez inflorescencias simples, en cimoides laxos. Flores tetrámeras, heterostilas, pilosas en el interior del tubo corolino. Frutos de dos mericarpos indehiscentes, con línea de dehiscencia preformada sobre la línea media de la cara adaxial. Semillas reticuladas o foveoladas con estrofíolo en la cara placentar. Granos de polen isopolares, radiosimétricos, entre 25–50 µm, oblato-esferoidales o prolato-esferoidales, estéfano-colporados, de exina semitectada-reticulada, con retículo complejo o simple (*Galianthe bogotensis* y *G. dichotoma*) (Pire, 1996). $2n = 28$ (*G. bogotensis*); $n = 15$ (*G. brasiliensis* subsp. *angulata*). [Los otros detalles bajo *G. brasiliensis* subsp. *angulata*.]

Clave para Diferenciar las Especies de *Galianthe* Subg. *Ebelia*

1a. Vaina estipular tubulosa, prolongada por encima de la inserción del par de hojas correspondiente.
  2a. Vaina pilosa; tallos de ángulos alados; Brasil ..... 9. *G. vaginata*
  2b. Vaina glabra; tallos sin alas; Brasil ..... 8. *G. polygonoides*
1b. Vaina estipular breve, no sobrepasando la inserción del par de hojas correspondiente.
  3a. Hojas sólo con el nervio medio visible.
    4a. Inflorescencias simples, en cimoide laxo, nudos floríferos con flores solitarias; Ecuador, Perú ..... 5. *G. dichotoma*
    4b. Inflorescencias compuestas, nudos floríferos con flores en fascículos o glomérulos.
      5a. Cáliz de 4 sépalos; inflorescencias compuestas cimoidales, inflorescencias parciales subglomeriformes; Colombia ..... 1. *G. bogotensis*
      5b. Cáliz de 2 ó 4 sépalos; inflorescencias compuestas, tirsoides-espiciformes o cimoidales, inflorescencias parciales en fascículos; México a Argentina ..... 2. *G. brasiliensis*
  3b. Hojas con nervios secundarios surcados en el haz y en resalto en el envés.
    6a. Inflorescencia cimoidal con inflorescencias parciales congestas, subglomeriformes.
      7a. Tallos de ángulos notoriamente alados; hojas 6–20 mm lat.; Brasil, Paraguay, Uruguay, Argentina ..... 4. *G. dichasia*
      7b. Tallos de ángulos oscuramente alados; hojas 1–7 mm lat.; Brasil .... 3. *G. cymosa*
    6b. Inflorescencia cimoidal de ramas cincinoides, con inflorescencias parciales paucifloras, fasciculadas.
      8a. Tallos simples; frutos sub-hemisféricos de 1.6–2 mm long.; Brasil, Paraguay, Argentina ... 6. *G. hispidula*
      8b. Tallos ramificados; frutos turbinados de 5 mm long.; Brasil ..... 7. *G. humilis*

1. Galianthe bogotensis (Kunth) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Spermacoce bogotensis* Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Quarto ed. 3: 347, Folio ed. 3: 271. 1819. *Diodia bogotensis* (Kunth) Cham. & Schltdl., Linnaea 3: 350. 1828. *Borreria bogotensis* (Kunth) Standl., Publ. Field Columbian Mus., Bot. Ser. 7: 160. 1930. TIPO: Colombia. Crescit juxta urbem Santa Fe de Bogotá, alt. 1370 hex, *Humboldt & Bonpland s.n.* (holótipo, B destruido; foto F860, CTES, SI; lectótipo, aquí designado, P). Figura 1.

A
2 cm
B
C
2 mm
D
E
2 mm
F
H
G
I
2 mm
J
K
1 mm

Borreria anthospermoides DC., Prodr. 4: 550. 1830. TIPO: Colombia. In Amer. austr. prope Sta.-Fe de Bogotá, colector desconocido, ex herb. Delessert, 1816 (holótipo, G; foto F6689, CTES, SI).

Sufrútice muy ramificado, semipostrado a postrado, formando una extensa mata, de tallos radicantes, estrechamente alados, glabros, escabriúsculos o pilósulos hacia el ápice de los entrenudos, con brotes axilares que dan apariencia verticilada a los nudos foliares. Hojas de 6–18 × 1.5–4 mm, angostamente elípticas u ovales, de base y ápice agudos y margen revoluto, sólo con la vena central manifiesta, subglabras, escabriúsculas sobre el margen, a veces algo sobre el haz y la vena media en el envés. Vaina estipular de 1–2.5 mm long., pubescente, con 5–7 lacinias de 2.5–4 mm long. Inflorescencia terminal cimoidal, con inflorescencias parciales, subglomeriformes, a veces en ramas laterales reducidas a 1 sola cabezuela. Cáliz con 4 segmentos triangulares y algún dientecito intercalar, sólo en los bordes escabriúsculos. Hipanto turbinado de 1.5–2.5 mm long., glabro a subglabro. Corola blanca, micropapilada en la superficie externa; disco entero. Flor brevistila: corola de 3.5–5 mm long., con lóbulos iguales o más cortos que el tubo corolino en su interior con pelos moniliformes cortos y delgados sobre el tubo y pelos gruesos sobre el tercio inferior de los lóbulos; anteras de 1–1.5 mm long. y filamentos estaminales de 0.6–1.2 mm long.; estilo de 1.5–3 mm long., de ramas estilares filiformes de 0.5–1.8 mm long. Flor longistila: corola de 4–5.5 mm long., de lóbulos más cortos que el tubo, de superficie interna con pelos dispersos sobre el tubo y pelos más densos, gruesos y largos en la base de los lóbulos; anteras de 1–1.3 mm long. y filamentos de 0.5–1 mm; estilo de 4–5 mm y ramas estilares de 2.5–0.9 mm long. Fruto de 2–3.2 mm long., glabro, de mericarpos indehiscentes. Semilla de 2–2.3 mm long., superficie foveolada, con ancho surco longitudinal en la línea media ventral, cubierto parcialmente por el estrofíolo.

Distribución (Fig. 11). Habita en el páramo o en área vecina en Colombia, entre 2200–3575 m s.m., en borde de ciénagas, matorral subserial, pastizal o rastrojos.

Material examinado. COLOMBIA. Nueva Granada, 1857, *Triana* 75 (NY, P). **Boyacá:** Cordillera Oriental, Páramo de Belén, 6 mayo 1959, *Barclay & P. Juajibioy 7573* y *7661* (MO, NY); Socha, 8 nov. 1944, *Fosberg 22225* (NY); Santuario de Yguaque, 26 mar. 1981, *Melampy 1313* (MO). **Cundinamarca:** Boquerón de Chipaque, 16 mar. 1939, *Killip 34201* (F, NY); Páramo de Guasca, 15 dic. 1938, *Balls 5696* (K); Páramo de Siberia, 25 oct. 1952, *Humbert et al. 26929* (SI); Macizo de Bogotá, 7 mayo 1946, *Schultes 7259* (F); Macizo de Bogotá, Quebrada de Chicó, 25 mayo 1939, *Cuatrecasas 5007* (F), dic. 1946, *Black 46-441* (F); Cordillera Oriental, Páramo, 16 nov. 1959, *García Barriga 16136* (NY); above Bogotá, 16 ago. 1917, *Rusby et al. 1260* (NY); 12 km WSW of Junín, on the Río Blanco, small affluent of the río Piedras, 19 Feb. 1944, *Fosberg 21484* (NY); Río San Francisco, above Bogotá, 13 set. 1917, *Pennell 1934* (NY); Sabana of Bogotá, supra hill, 4 Feb. 1945, *Schiefer 402* (F); Bogotá, Nov. 1852, *Holton 417* (K), 29 Oct. 1975, *André 728* (K); above La Cita, 10 mayo 1946, *Schultes 7122* (F); près de Bogotá, *Triana 3123* (P); Boquerón de Bogotá, 21 nov. 1975, *André 72* (K); Bogotá, 20 set. 1913, *Apolinar 74* (F); Montecillo E of Guatavita, 29 mayo 1947, *Haught 5774* (F); Paipa, ene. 1938, *Jimenez 68* (F).

Esta especie se parece por sus inflorescencias a *G. cymosa* y *G. dichasia*, pero se diferencia de ambas por sus hojas más pequeñas y subenervias. Su área está restringida a los páramos de Bogotá y zonas circunvecinas, mientras que las otras dos especies son del SE del Brasil, la primera citada sólo para el estado de Paraná y la segunda desde Paraná llega hasta el Paraguay, Argentina y Uruguay; ambas de terrenos bajos y húmedos.

2. Galianthe brasiliensis (Spreng.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Diodia brasiliensis* Spreng., Syst. Veg. 1: 406. 1824. TIPO: Brasil, Sello (holótipo, B destruido); Brasil. Sin loc., año 1828, *Pohl s.n.* (neótipo, aquí designado, G; foto F6728, SI).

Subarbusto de 0.30–0.70(–1) m de alto. Tallos tetrágonos, de ángulos marginados a estrechamente alados, glabros a hírtulos. Hojas opuestas, o en general seudoverticiladas, 3–35 × 0.7–11 mm, ovadas o elípticas, agudas, atenuadas en seudopecíolo, escabriúsculas en el margen y los nervios en el envés a glabras, nervadura poco visible, con excepción del nervio medio; vaina estipular 3–7 laciniada, glabra o hispídula. Inflorescencia frondosa a bracteada, tirsoide, espiciforme a pleiotirsoide con inflorescencias parciales también espiciformes o cimoidal, de ramificación dicasial a monocasial, siempre con flores congestas, fasciculadas en los nudos floríferos. Flores brevemente pediceladas. Cáliz 2 ó 4 partido, con dientecitos intercalares. Hipanto turbinado, glabro o hírtulo. Corola

←

Figura 1. *Galianthe bogotensis.* —A. Rama. —B. Vaina estipular. —C–E. Flor longistila. —F–H. Flor brevistila. —I. Fruto. —J. Mericarpo. —K. Semilla no madura. A–E, *García Barriga 16136*; F–H, *Fosberg 20268*; I–K, *Melampy 1313.*

4-lobada, 2–3.5 mm long., algo pilosa en su interior. Flor brevistila: anteras 1–1.25 mm, filamentos estaminales 1 mm y estilo 1.3–1.5 mm long. Flor longistila: anteras 0.5–1 mm, filamentos estaminales muy breves y estilo 2.5–3.5 mm long. Fruto 1.5–2.5 mm long., turbinado, algo comprimido lateralmente, hispídulo. Semilla 1–2 mm long., finamente reticulada, reniforme en corte transversal, con leve y amplia depresión longitudinal cubierta por el estrofíolo.

Esta especie cubre dos áreas de dispersión, una amplia en Sudamérica, desde Bahia a Rio Grande do Sul en Brasil, Paraguay, Uruguay y NE de la Argentina hasta la ribera bonaerense del Río de La Plata. La otra área está restringida al S de México, Belice y Guatemala. En relación con la distribución se puede señalar que el material de México y áreas vecinas es uniforme en sus caracteres, no así el sudamericano que presenta variaciones principalmente en el tamaño de las hojas, a veces en un mismo ejemplar, en el desarrollo de las inflorescencias y en el número de los segmentos del cáliz. Las mismas han sido registradas por los autores en distintas variedades, las cuales resultan difíciles de reconocer en su mayoría por las transiciones observadas en los ejemplares estudiados. Hasta donde se ha podido estudiar los ejemplares con cáliz 2 ó 4-mero se corresponden con inflorescencias algo diferentes. Las muestras con cáliz de 2 segmentos mayores presentan inflorescencias tirsoide-espiciformes o pleiotirsoides con paracladios también espiciformes. Las muestras con cáliz 4-partido, de segmentos similares, presentan inflorescencias tirsoides pero en parte con ramificación cimoidal, con paracladios que superan el eje principal. En ambos casos los nudos floríferos tienen flores fasciculadas. De ahí que en el presente trabajo y hasta tanto no se realize una revisón más completa, principalmente de los herbarios brasileños, se propone aceptar a todo el material sudamericano como *G. brasiliensis* subsp. *brasiliensis*, y con respecto al material de México, Belice y Guatemala, aceptarlo como *G. brasiliensis* subsp. *angulata* (Benth.) E. L. Cabral & Bacigalupo, por sus caracteres uniformes y área restringida.

CLAVE PARA DIFERENCIAR LAS SUBESPECIES DE *GALIANTHE BRASILIENSIS*

1a. Cáliz 2 ó 4-partido; inflorescencias tirsoide-espiciformes o de ramificación parcialmente cimoidal, con el eje principal más corto que los laterales; Sudamérica ..... subsp. *brasiliensis*

1b. Cáliz 4-partido; inflorescencias notoriamente tirsoide-espiciformes; México, Centroamérica ..... subsp. *angulata*

2a. Galianthe brasiliensis subsp. **brasiliensis** (Fig. 2)

Diodia anthospermoides Cham. & Schltdl., Linnaea 3: 343. 1828. *Triodon anthospermoides* (Cham. & Schltdl.) DC., Prodr. 4: 566. 1830. *Diodia polymorpha* var. *anthospermoides* (Cham. & Schltdl.) K. Schum., in Mart., Fl. Bras. 6(6): 12. 1888. TIPO: Brasil. In Brasilia aequinoctiali, Sellow (holótipo, B destruido); Brasil. Rio de Janeiro: 1883–84, *Glaziou 14926* (neótipo, aquí designado, K).

Diodia polymorpha Cham. & Schltdl., Linnaea 3: 344. 1828. TIPO: Brasil. E Brasilia tropica extratropica magnam speciminum varieta tumque copiam misit Sellow (holótipo, B destruido); Brasil. Paraná: Mato Preto, *G. Hatschbach 33869* (neótipo, aquí designado, MBM; isoneótipo, SI).

Diodia polymorpha var. *macrophylla* Cham. & Schltdl., Linnaea 3: 345. 1828. TIPO: Brasil. E Brasilia meridionali, Sellow (holótipo, B destruido); Argentina. Entre Ríos: Concepción del Uruguay, *Lorentz 1799* (neótipo, aquí designado, CORD).

Diodia polymorpha var. *microphylla* Cham. & Schltdl., Linnaea 3: 345. 1828. *Triodon polymorphus* var. *microphyllus* (Cham. & Schltdl.) DC., Prodr. 4: 566. 1830. *Diodia polymorpha* var. *microphylla* (Cham. & Schltdl.) Standl., Publ. Field Columbian Mus., Bot. Ser. 8: 387. 1931. TIPO: Brasil. E provincia Rio Janeiro proveniens, Sellow (holótipo, B destruido; lectótipo, aquí designado, K material estéril).

Triodon glomeratus DC., Prodr. 4: 566. 1830. TIPO: Brasil. In Brasilia, *Pohl s.n.* (holótipo, G; foto F6728, SI).

Sufrútice con hojas de 3–35 mm long. × 0.7–11 mm lat., elípticas, a veces algunas obovadas. Inflorescencias tirsoide-espiciformes o pleiotirsoides con paracladios espiciformes, nudos floríferos con flores fasciculadas. Cáliz de 4 segmentos subiguales o 2 segmentos mayores y dientecitos intercalares mucho menores.

Distribución (Fig. 11). Brasil, Paraguay, Uruguay y NE de la Argentina hasta el delta del río Paraná y costa ribereña de Buenos Aires.

Material seleccionado. BRASIL. **Bahía:** Munic. do Livramento do Brumado, Río Contas, 19–20 jul. 1979, *Mori et al. 12310* (K); Río do Contas, Salto do Fraga, 6 abr. 1992, *Hatschbach 56688* (CTES). **Minas Gerais:** sin fecha, *Widgren 199* (K); Poços de Caldas, Veu das Noivas, 19 ene. 1980, *Krapovickas et al. 35396* (CTES); São Thome das Letras, Serra do Cantagalo, 3 nov. 1984, *J. Pirani et al. s.n.* (CTES, K, SPF). **Paraná:** Serra do Mar, Porto do Cima, 2 ene. 1914, *Dusén 14297* (K); Mun. Iguazú, 20 ene. 1949, *Schwarz 7239* (CTES); Ríos dos Patos, 27 mar. 1947, *Hatschbach 668* (CTES); Fernandes Penheiro, 27 mar. 1904, *Dusén 4331* (SI). **Rio de Janeiro:** abr. 1875, *Glaziou 7671* (K), abr. 1975, *Glaziou 7670* (K), Serra do Itataia, sin fecha, *Pereira 7088* (LP). **Rio Grande do Sul:** Parecí prope Montenegro, 31 mar. 1950, *Rambo 46526* (K); Alegrete, Río Ibira Puitan, 13 mar. 1948, *Palacios-Cuezzo 1829* (CTES); São Sepe, 22 feb. 1948, *Palacios-Cuezzo 1555* (CTES); Cachoeira do Sul, 19 feb. 1948, *Palacios Cuezzo 1068* (CTES); Arroio dos Ratos, dic. 1973, *Mariath 150* (CTES); Morro do Coco, 20 jun. 1973, *Lindeman et al s.n.* (CTES, ICN), 21 abr. 1974, *Porto 595* (CTES). **Santa Catarina:** Munic. Ybirama, *Smith et al. 7599* (K). **São Paulo:** Munic. São Paulo, Inst. de Botánica, 17 ene. 1968, *Eiten 8090* E (K); Inter Muggy et São

Figura 2. *Galianthe brasiliensis* subsp. *brasiliensis*. —A. Rama. —B, C. Flor longistila. —D, E. Flor brevistila. —F. Fruto. —G–I. Semilla, cara ventral, perfil y corte transversal. A, *Burkart 4492*; B, C, *Burkart 20002*; D, E, *Burkart 18202*; F–I, *Burkart 3844*.

Paulo, nov. 1833, *Riedel 1518* (K); Mun. de Campos do Jordão, 20 mar. 1969, *Souza s.n.* (CTES). PARAGUAY. In regione lacus Ipacaray, Nov. 1913, *Hassler 12709* (G). **Alto Paraná:** Puerto Gibajas, 28 mar. 1970, *Krapovickas et al. 15765* (CTES); Irala, 23 nov. 1950, *Montes 9866* (CTES); Pto. Indio, 6 set. 1981, *Caballero Marmori 889* (CTES). **Itapúa:** Encarnación, 18 ene. 1944, *Rojas 10889* (CTES), 19 nov. 1945, *Bertoni 2401* (CTES); Isla Yaciretá, 3 feb. 1982, *Bordas 3039* (CTES). URUGUAY. Fray Bentos, 14 feb. 1877, *Fruchard s.n.* (P). ARGENTINA. **Misiones:** Apóstoles, San José, Escuela Agrotécnica P. Gentilini, potrero San Lorenzo, 12 feb. 1973, *Cabrera & Sáenz 29137* (SI); Cainguás, Puerto Rico, 4 mar. 1948, *Schwindt 629* (CTES); Candelaria, Ruinas Jesuíticas de Sta. Ana, 29 jun. 1986, *Ferrucci et al. 436* (CTES); Capital, Posadas, costa del río, 24 nov. 1949, *Bertoni 4796* (CTES); Guaraní, Ayo. Paraiso y Ruta 2, 23 set. 1993, *Rodríguez et al. 763* (CTES, MNES); Iguazú, Parque Nacional Iguazú, 7 ago. 1991, *Vanni et al. 2751* (CTES); San Ignacio, Teyucuaré, 4 abr. 1946, *Montes 2100* (CTES); San Pedro, Ayo. Liso, 22 set. 1945, *Bertoni 2076* (CTES). **Corrientes:** Berón de Astrada, Tuyuty, 3 mayo 1945, *Huidobro 2137* (CTES); General Paz, 12 km E de Itá Ibaté, costa del río Paraná, *Mroginski et al. 680* (CTES); Itatí, 18 abr. 1971, *Mroginski 149* (CTES); Santo Tomé, Ea. Timbó, 2 mar. 1983, *Schinini et al. 23794* (CTES); Ituzaingó, Empalme Ruta 34 y Ruta 14, 22 feb. 1980, *Cabral 160* (CTES); San Cosme, Paso de la Patria, 17 jun. 1945, *Worth 130* (CTES). **Entre Ríos:** Concordia, Salto Grande, 20 dic. 1961, *Burkart 23139* (SI); Gualeguaychú, Delta, arroyo Brazo Largo, mar. 1937, *Burkart 8298* (CTES, SI); Gualeguaychú, Landa, *Soriano 393* (BAB). **Buenos Aires:** Delta del Paraná, Paraná de las Palmas y Canal 6, 20 oct. 1938, *Mollura 17* (SI); Isla Martín García, 2 mayo 1948, *Soriano s.n.* (SI 22704).

2b. Galianthe brasiliensis subsp. **angulata** (Benth.) E. L. Cabral & Bacigalupo, stat. nov. Basónimo: *Triodon angulatum* Benth., Pl. Hartw.: 70. 1840. *Diodia polymorpha* var. *angulata* (Benth.) K. Schum., in Mart., Fl. Bras. 6(6): 13. 1888. *Diodia brasiliensis* var. *angulata* (Benth.) Standl., Carnegie Inst. Wash. Publ. 461: 90. 1935. TIPO: México. Textolcingo in montibus Chinantla, *Hartweg 507* (holótipo, K no visto). Figura 3.

Arbusto de tallos algo hispídulos, ángulos estrechamente alados, glabros. Hojas 5–18 mm × 1.5–

Figura 3. *Galianthe brasiliensis* subsp. *angulata*. —A. Rama. —B. Vaina estipular. —C. Detalle de la inflorescencia. —D–F. Flor brevistila. G–I. Flor longistila. —J. Fruto. —K. Semilla. A, *Schnee & Maury s.n.*; B–F, *Avendano et al. 00446*; G–I, *Breedlove 52678*; J, K, *Turckheim II-1605*.

6 mm, elípticas u obovadas, de haz glabro y envés ralamente escabriúsculo sobre el nervio medio y secundarios; vaina estipular hispídula, con 5–7 lacinias glabras. Inflorescencias tirsoides espiciformes, con 4 a 14 nudos floríferos, o pleiotirsoides. Cáliz 4-partido, con 2 segmentos opuestos ligeramente mayores, de 0.8–1 mm long., y algún dientecito en los senos intercalares. Hipanto turbinado, hispídulo. Flor longistila: corola 1.9–2.2 mm long., anteras 0.4–0.5 mm y filamentos estaminales 0.17–0.2 mm long., estilo 2 mm long. Flor brevistila: corola 2.7 mm long., anteras 0.6–0.7 mm y filamentos estaminales 1.15 mm; estilo 3–3.15 mm. Fruto 1.5(–2.5) mm long., hispídulo. Semilla 1.8–2 mm long.

Nombre vulgar. Tomillo silvestre.

Distribución (Fig. 11). Sur de México, Guatemala, Belice. Se la encuentra a 1350–1700 m s.m. Burger y Taylor (1993) citan la especie para Costa Rica pero dudan de que sea nativa en ese país.

Material examinado. GUATEMALA. **Alta Verapaz:** Cobán, ene. 1907, *von Türckheim 111605* (BAF, SI). **Petén:** San Luis, 10 jul. 1959, *Lundell 16271* (CTES). BELICE. **El Cayo:** Sibun River, 23 jun. 1955, *Gentle 8773* (CTES). MEXICO. Sin localidad, *Linden 615* (BR). **Chiapas:** Rayón, in the Selva Negra, 10 km above Rayón Mezcalapa along road to Jitotol, 10 Sep. 1981, *Breedlove 52678* (NY). **Hidalgo:** El Candeje, 4 jun. 1973, *Gimate 852* (CTES). **Veracruz:** Munic. de Totutla, 7 jul. 1977, *Ventura 14223* (G); Jicó, 5 jul. 1908, *Pringle 10803* (CTES); Tenejapa, 2 ago. 1979, *Avendano et al. 00446* (NY); environs d'Orizaba, *Botteri & Sumichrast 186* (P); Valle de Córdoba, 10 dic. 1865–66, *Bourgeau 1716* (BR, P); Córdoba, 4 ago. 1882, *Kerber 23* (BR). Sin dato de localidad ni fecha de colección, *Schnee & Maury s.n.* (P, SI).

Lewis (en Kiehn, 1986) registró, bajo el nombre de *Triodon angulatum*, como número cromosómico para esta especie $n = 15$ sobre un ejemplar de Veracruz, México.

3. Galianthe cymosa (Cham.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Diodia cymosa* Cham., Linnaea 9: 217. 1834. TIPO: Brasil. E Brasilia tropica misit Sellow (holótipo, B destruido; foto F 861 CTES, SI); Brasil. Paraná: Pinhais, 20 mar. 1952, *Tesmann et al. 749* (neótipo, aquí designado, MBM). Figura 4.

Sufrútice apoyante de 50–65 cm alt., con tallos gráciles, tetrágonos pubérulos a glabros, con alas muy estrechas, retrorso-escabriúsculas sobre los márgenes. Hojas angostamente elípticas, 10–35 × 1–7 mm, ápice acuminado y base atenuada, con 3 pares de nervios secundarios, subopuestos, escabriúsculas en la haz y sólo sobre los nervios en el envés margen revoluto, escabriúsculo. Vaina estipular 2–2.5 mm long., pubérula, pelos más largos y densos hacia el margen, lacinias 5–6, glabras de 1–5 mm long. Inflorescencia cimoidal, dicasial a monocasial, con inflorescencias parciales densas, subglomeriformes. Cáliz 4 segmentos, 2 de 2.5–3 mm y 2 menores de 1.5–2 mm, con algunos dientes intercalares. Hipanto glabro, obcónico, 1.6–2 mm long. Corola externamente micropapilada, con papilas notables en el dorso apical de los lóbulos, superficie interna, con anillo de pelos moniliformes en la base de los lóbulos y pelos dispersos sobre el tubo, lóbulos más cortos que el tubo. Flor brevistila: corola 4.5–6.2 mm long., anteras 1.2–1.5 mm, filamentos estaminales 1.2–2 mm, estilo 2.5–3.5 mm y ramas estilares de 1–2 mm long., densamente papilosas. Flor longistila: corola 5–6 mm long., anteras 1.3–1.5 mm, estilo 5–6 mm y ramas estilares de 0.8–1 mm long. Fruto obcónico, glabro, 3–4 mm long. Semilla más o menos plano-convexa, 2 mm long., escrobiculada, con estrofíolo cubriendo parcialmente la cara ventral.

Distribución (Fig. 11). Hasta el momento se la ha coleccionado solo en el Estado de Paraná, Brasil.

Material examinado. BRASIL. **Paraná:** 1833, *Gaudichaud 518* (G); Serrinha, in campo, 14 ene. 1904, *Dusén 2695* (G); Curitiba, Barigui, 28 ene. 1975, *Ferreira 186* (MBM, MO, NY, US); Mandirituba, río Mauricio, 23 feb. 1978, *Hatschbach 41460* (US).

Esta especie guarda estrecha relación con *Galianthe dichasia* por su porte y sus inflorescencias, pero ésta presenta tallos con alas desarrolladas y hojas más anchas.

4. Galianthe dichasia (Sucre & C. G. Costa) E. L. Cabral, Bol. Soc. Argent. Bot. 27: 242. 1991. Basónimo: *Borreria dichasia* Sucre & C. G. Costa, Loefgrenia 48: 2. 1970. TIPO: Brasil. Estado do Paraná: Curitiba, Aeroporto Affonso Penna, *Pereira 5158* (holótipo, RB; isótipo, HB). Figura 5.

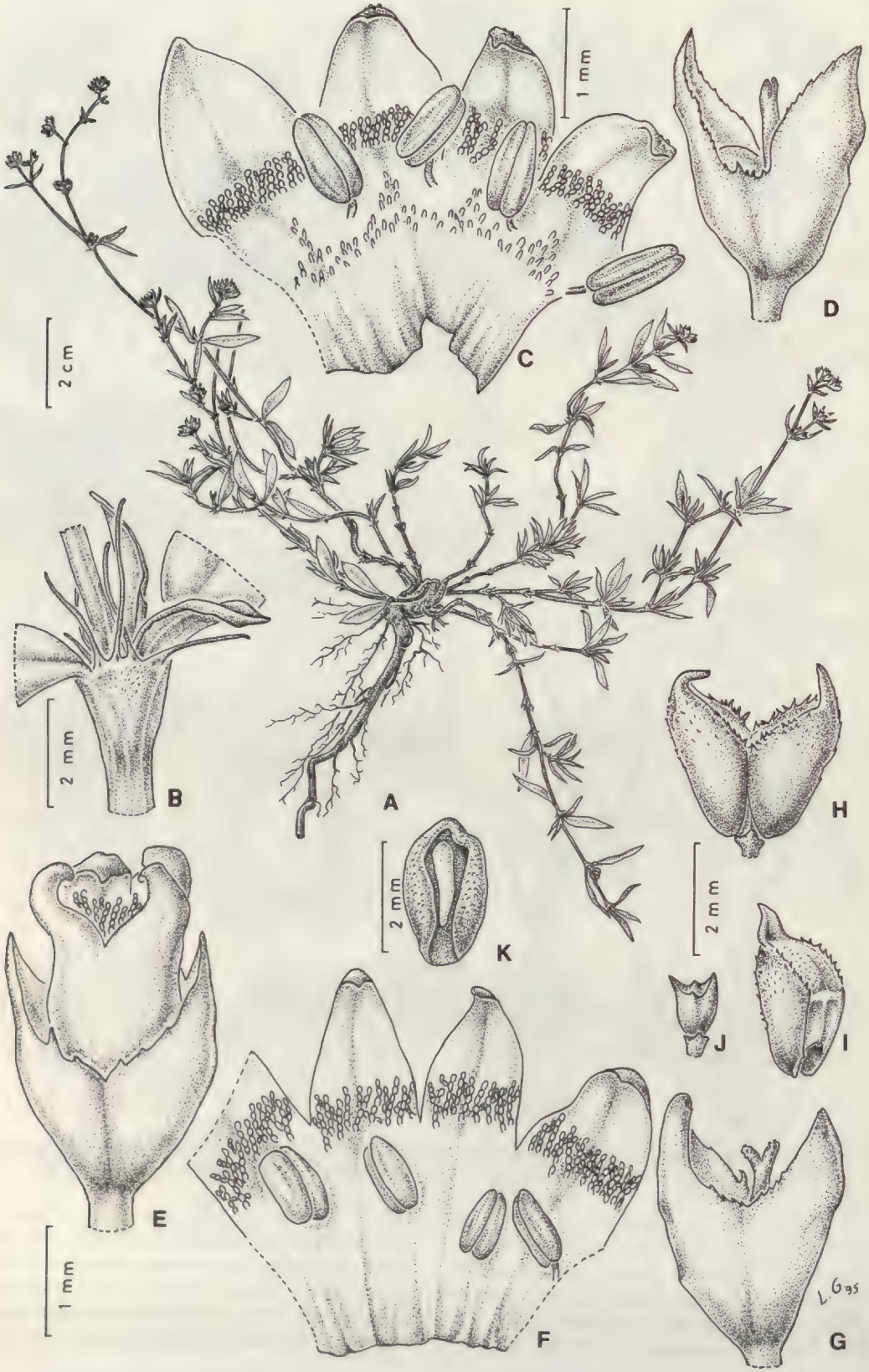
Diodia cymosa Cham. var. *aculeolata* Hassl., Feddes Repert. Spec. Nov. 14: 168. 1915. TIPO: Paraguay. Guairá: Cordillera de Villa Rica, I-1905, *Hassler 8650* (lectótipo, aquí designado, G; isolectotipo, NY).

Hierba sufruticosa de 50–80 cm de alt., erecta, de tallos radicantes los nudos basales, tetrágonos, fistulosos, ± hirsutos o glabros con ángulos muy marcados hasta alados, alas de 1.7 mm de ancho, retrorso-laciniadas en el margen. Hojas elípticas, 15–60 × 6–20 mm, de ápice agudo o acuminado y base atenuada, pilosas, escabriúsculas a subglabras en ambas caras, margen revoluto, con 3–5 pares de nervios subopuestos, impresos en el haz y

Figura 4. *Galianthe cymosa.* —A. Planta. —B. Vaina estipular. —C–E. Flor brevistila. F–H. Flor longistila. —I. Fruto. A–E, *Tesmann et al. 749*; F–I, *Dusén 2695.*

Figura 5. *Galianthe dichasia.* —A. Planta. —B. Vaina estipular. —C. Corte del tallo. —D–F. Flor brevistila. —G–I. Flora longistila. —J. Fruto. —K. Mericarpo. A–F, J, K, *Krapovickas et al. 44888*; G–I, *Imaguire 2781.*

en resalto en el envés. Vaina estipular pilosa, 3–5 mm long., 5–7 lacinias glabras, de 2–10 mm long. Inflorescencia cimoidal, dicasial a monocasial, con inflorescencias parciales subglomeriformes. Cáliz de 4 segmentos aleznados, 1.6–2.8 mm, a veces 2 ligeramente menores, opuestos, a menudo con diminutos dientecitos intercalares, glabros, de borde escabriúsculo, hipanto obcónico 1–1.5 mm long., glabro. Corola blanca, externamente micropapilada, con papilas notables en el dorso apical de los lób-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ulos, estos más cortos que el tubo, superficie interna con dos anillos de pelos moniliformes, uno sobre el tubo y otro de pelos algo más gruesos sobre la base de los lóbulos; disco entero. Flor brevistila: corola 4–5.2 mm, anteras 1–1.2 mm, filamentos estaminales 0.5–1.5 mm, estilo 2.5–4.7 mm, ramas estigmáticas de 2–2.2 mm de largo, con papilas densas. Flor longistila: corola 3.7–5 mm, anteras 0.7–1 mm, filamentos estaminales 0.2 mm y estilo de 4–5.8 mm long. Fruto 2.5–3.5 mm long. Semilla 2 mm de largo, plano-convexa con estrofíolo cubriendo parcialmente la cara ventral.

Distribución (Fig. 11). Esta especie vive en terrenos bajos, pantanosos, orilla de vertientes. Su área abarca el SE del Brasil (Paraná, Sta. Catarina y Rio Grande do Sul), Paraguay (San Pedro, Guairá), Uruguay (Rivera) y Argentina (Misiones).

Material examinado. BRASIL. **Paraná:** Rincao, 9 feb. 1947, *Hatschbach 624* (CTES, SP); Curitiba, 28 mar. 1950, *Tessmann 67* (MBM); 5 km E de Curitiba, 2 feb. 1973, *Krapovickas et al. 23093* (CTES, LP), 14 feb. 1978, *Krapovickas et al. 33657* (CTES); Piraquara, 3 mar. 1971, *Imaguire 2781* (ICN), 31 ene. 1967, *Dombrowski 2391* (CTES). **Santa Catarina:** Caçador, 22 dic. 1956, *Smith et al. 9073* (R). **Rio Grande do Sul:** Torres, Lagoa dos Quadros, 21 feb. 1950, *Rambo 45992* (CTES, LIL); Farroupilha, 7 feb. 1950, *Rambo 45708* (CTES); Caxias do Sul, 8 feb. 1955, *Rambo 56689* (PACA), 1 ene. 1949, *B. Rambo 30882* (PACA), 1932, *Augusto s.n.* (PACA); S. Leopoldo, 1907, *Theissen s.n.* (PACA); Bom Jesús, 13 ene. 1941, *B. Rambo 8521* (PACA), 15 ene. 1942, *Rambo 8839* (PACA); Ijuisinho, 30 ene. 1942, *Rambo 9961* (PACA); Cambará, feb. 1948, *Rambo 36712* (PACA). PARAGUAY. **San Pedro:** 10 km W de San Estanislao, bañado del río Tapiracuí, 19 feb. 1994, *Krapovickas et al. 44888* (CTES). URUGUAY. **Rivera:** Cunapirú, p. Rivera, 13 ene. 1941, *Rambo 3973* (PACA). ARGENTINA. **Misiones:** Gral. Belgrano, Ao. Pepirí Guazú, ene. 1983, *Guaglianone et al. 1147* (CTES, SI); Ldor. Gral. San Martín, Ao. Garuhapé, *Mroginski et al. 378* (CTES).

Galianthe dichasia guarda estrecha relación con *G. cymosa* de la que se diferencia por sus tallos más robustos, de ángulos bien marcados a manifiestamente alados y sus hojas anchas.

5. Galianthe dichotoma (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Knoxia dichotoma* Willd. ex Roem. & Schult., Syst. Veg. 3: 532. 1818. TIPO: América meridionalis. Humboldt (holótipo, B no visto, foto B-W 2676, F 862, CTES, SI). Figura 6.

Diodia glabra Willd. ex Roem. & Schult., Syst. Veg. 3: 532. 1818, non Pers. (1805).

Spermacoce dichotoma Willd. ex Kunth, in Humb., Bonpl. & Kunth, Nov. Gen. Sp. Quarto ed. 3: 348; Folio ed. 3: 272. 1819. *Borreria dichotoma* (Willd. ex Kunth) Cham. & Schltdl., Linnaea 3: 340. 1828. *Diodia dichotoma* (Willd. ex Kunth) K. Schum., in Mart., Fl. brasil. 6 (6): 11. 1888. TIPO: Perú. Prope Peruvianorum et in declivitate montis ignivomi Tunguraguae, alt. 1400–1600 hex, Bonpland (holótipo, P, foto F37152, CTES, SI).

Triodon laxum [*Triodia laxa*] Bentham, Pl. Hartw.: 194. 1840. TIPO: Juxta ponte Guapulo, prope Quito, *Hartweg 1068* (holótipo, K no visto).

Sufrútice con ramas postradas de 10–30 cm long., tallos tetrágonos con alas estrechas, de margen escabriúsculo. Hojas ovales, de 7–20 × 2–7 mm, ápice acuminado y base atenuada en corto seudopecíolo, margen revoluto, escabriúsculo, discoloras, haz escabriúscula a glabra, con vena media surcada, poco conspicua, envés escabriúsculo sobre la vena media sobresaliente, y a veces sobre los 2–3 pares de nervios poco conspicuos. Vaina estipular 1.7–3.5 mm long., pilosa, con 3–7 lacinias glabras, de 1.5–4 mm long. Inflorescencia cimoide, dicasial, con brácteas foliáceas en los nudos basales, disminuyendo a linear-subuladas, diminutas en nudos apicales. Cáliz bipartido, de 2 segmentos triangulares, carnosos, de bordes escabriúsculos, casi siempre alternando con algunos dientecitos intercalares; hipanto obcónico, 1–1.2 mm long., escabriúsculo en la mitad superior. Corola 4(–5)-lobada, 2.5–3.8 mm long. de lóbulos más cortos que el tubo, micropapilada por fuera, con papilas notables en el dorso apical de los lóbulos y con pelos moniliformes en su interior. Anteras 0.7–0.8 mm long. y filamentos breves. Estilo 0.5–1.2 mm long., con ramas de 0.5 mm long. Fruto turbinado 3–3.5 mm long., escabriúsculo a subglabro. Semilla 2.5–3 mm long., subobovoide, de superficie foveolada, con estrecho surco en la cara ventral cubierto parcialmente por el estrofíolo.

Distribución (Fig. 11). Habita en zonas altas, entre los 2300–3340 m s.m. en Ecuador hasta el norte de Perú.

Material examinado. ECUADOR. **El Oro:** Hacienda Chepel, headwaters of Río San Luis, 22 km E of Zaruma, 13 Feb. 1945, *Fosberg & Giler 23007* (NY). **Loja:** upper Malacatos Valley, 15–20 km S Loja, 6 July 1944, *Prieto 36* (NY); Paso de Cajanuma above Pueblo Nuevo, 9 feb. 1945, *Fosberg & Giler 22889* (P); Loja, W of town, 3 Oct.

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Figura 6. *Galianthe dichotoma.* —A. Planta. —B. Vaina estipular. —C, D. Flor longistila. —E–G. Flor brevistila. —H. Fruto. —I. Mericarpo. —J. Base del fruto. —K. Semilla no madura, cara ventral. A–D, H–K, *Cerón 2253*; E–G, —H. Fruto. —I. Mericarpo. —J. Base del fruto. —K. Semilla no madura, cara ventral. A–D, H–K, *Barclay et al. 8454.*

1955, *Asplund 17894* (G, P); San Pedro Loja, 26 abr. 1946, *Espinosa 246* (NY). **Pichincha:** Cantón Quito, Parroquia Calacali, Reserva Geobotánica Pululahua, alrededores de Pailon, 25 sep. 1987, *Cerón 2253* (CTES, MO); ad margen viae ad flumen Machángara pr. Quito, 16 abr. 1920, *Holmgren 522* (G); côté de Guápulo, 20 mar. 1930, *Benoist 2195* (P); in Andibus Ecuadorensibus, 1861, *R. Spruce 5997* (G); vicinity of Guápulo, 31 mayo 1939, *Asplund 6639* (G, P); Quito, sin fecha, *Jameson 792* (G). PERU. Sin localidad, sin fecha, *Mattheros 1502* (BR). **Amazonas:** Leimabamba, 13 dic. 1962, *Woytkowski 7757* (MO). **Cajamarca:** camino a la Laguna Chamis, 11 jun. 1971, *Sánchez Vega 759* (CTES, SI). **La Libertad:** Sartimbamba, Marcabal, 26 feb. 1949, *Infantes Vega 1902* (LIL), 18 ago. 1952, *Infantes Vega 3738* (LIL).

En esta especie no se manifiesta un claro dimorfismo floral, pero se incluye en el subg. *Ebelia* por sus inflorescencias de ramificación cimosa y sus frutos de mericarpos indehiscentes.

6. Galianthe hispidula (A. Rich. ex DC.) E. L. Cabral & Bacigalupo, comb. nov. Basónimo: *Diodia hispidula* A. Rich. ex DC., Prodr. 4: 565. 1830. TIPO: Brasil. Brésil Leandro do Sacramento 103, año 1819 (holótipo, P no visto, foto F37153 CTES, SI). Figura 7.

Diodia paradoxa Cham., Linnaea 9: 216. 1834. TIPO: Brasil. Brasilia, Sellow (holótipo, B destruido, foto F869, CTES, SI); Brasil. Minas Gerais: 23-I-1846, *Widgren 1025* (neótipo, aquí designado, BR).

Sufrútice rizomatoso, de tallos simples, de 30–60 cm de alt., tetrágonos, alados, glabros o ralamente pilosos sobre los ángulos o con escasas emergencias o lacinias con pelo apical. Hojas 35–100 × 15–35 mm, discoloras, vinosas al envejecer, elípticas u ovales, de ápice agudo o acuminado y base obtusa, atenuada en seudopecíolo, con 5–8 pares de nervios secundarios, ligeramente curvos y paralelos, haz glabra o escabriúscula sobre toda la lamina o sólo sobre los nervios y bordes; vaina estipular escabriúscula o pilosa, con 5–9 lacinias hasta 10–13 mm long., glabras o algo escabriúsculas en la base. Inflorescencia cimoidal, monocasial a pleiocasial, con paracladios en gran parte cincinoides, con inflorescencias parciales contraidas, fasciculadas. Flores hipanto turbinado, escabriúsculo. Cáliz 4-partido, de 2 sépalos de 2.5–3 mm long, triangular-subulados, alternando con otros 2 sépalos menores y algún dientecito intercalar, glabro, de borde escabriúsculo, o rara vez también con alguna papila en el dorso de los sépalos. Corola blanca, 4-lobada, 3.8–4.6 mm long., de lóbulos más cortos que el tubo. Flor brevistila: superficie interna de la corola con pelos dispersos sobre el tubo y base de los lóbulos, anteras 0.8–1.2 mm long., estilo 0.8–1.6 mm long. y ramas estilares de 1 mm. Flor longistila: superficie interna de la corola, con pelos moniliformes gruesos sobre los lóbulos y delgados sobre el tubo; anteras 0.8 mm long., estilo 3.5–4.5 mm long., ramas estilares de 1–1.2 mm. Fruto subhemiesférico, 1.6–2 mm long., de superficie escabriúscula a glabra. Semilla de color castaño oscuro, 1.4–1.6 mm long., con estrofíolo rodeado por surco profundo.

Distribución (Fig. 11). Hierba umbrófila, habita en bosques y selvas del sur del Brasil, Paraguay y NE de la Argentina. Florece y fructifica desde la primavera hasta entrado el otoño.

Material seleccionado. BRASIL. **Minas Gerais:** Caldas, *Regnell I 178* (P), 1845, *Widgren 202* (K); Bandeira do Sul, 20 ene. 1980, *Krapovickas et al. 35405* (CTES). **Paraná:** Porto Helena, 1 feb. 1949, *Schwarz 7425* (CTES); Campo Nov. Laranjeiras do Sul, 8 dic. 1968, *Hatschbach 20563* (NY). **Rio de Janeiro:** Nova Friburgo, morro da Caledonia, 8 jun. 1977, *Martinelli 2538* (RB). **Rio Grande do Sul:** Reserva Nonoai, 7 dic. 1974, *Porto 1186* (CTES, ICN). **Santa Catarina:** Itapiranga, San Antonio, 12 nov. 1964, *L. Smith et al. 13193* (LP), 6 feb. 1951, *Rambo 49879* (US). PARAGUAY. **Alto Paraná:** Irala, 1 dic. 1950, *Montes 11101* (CTES, LP). ARGENTINA. **Misiones:** in distr. urb. Posadas, praecipue in vicin. coloniae Bonpland, sin fecha, *W. Lillieskold s.n.* (G); L. N. Alem, Alem, Camping Municipal, 22 nov. 1986, *Cabral et al. 496* (CTES); Gral. Belgrano, San Antonio, nov. 1949, *Grondona et al. 3273* (BAB); Cainguás, Ayo. Cuna, Pirú, 8 km de A. del Valle hacia Jardín de América, 8 dic. 1983, *J. Hunziker et al. 10896* (SI); Ayo. Solito, nov. 1949, *Martínez Crovetto & Leguizamón 5834* (BAB, SI); Candelaria, Bonpland, Ayo. Mártires, 18 dic. 1983, *Cabral et al. 431* (CTES), 18 mayo 1909, *Jörgensen 27* (BAB); Guaraní, El Paraiso y Ruta 2, 23 set. 1993, *Rodríguez et al. 754* (CTES); Orilla R. Bonito, 8 km desembocadura R. Uruguay, 7 dic. 1983, *Hunziker et al. 10824* (CTES); 14 km de El Soberbio, 6 dic. 1983, *Hunziker et al. 10801* (SI); Iguazú, Reserva Apepú, 4 mar. 1982, *Ferraro 2463* (CTES); Ayo. Uruguaí, nov. 1949, *M. Crovetto et al. 5777* (BAB, SI); Parque Nacional Iguazú, 11 ene. 1972, *Mroginski et al. 300* (CTES), 1 dic. 1993, *Vanni et al. 3082* (CTES), 15 nov. 1976, *Guaglianone 174* (SI); 8 km del cruce de Libertad, Salto Uruguaí, 9 dic. 1983, *Hunziker et al. 10903* (SI); Ayo. Uruguaí, 35 km de Pto. Bemberg, 5 feb. 1951, *Capurro 868* (BA); Río Uruguaí, Yacú Poí, 25 oct. 1949, *Perrone* (BA 54548), 28 nov. 1884, *Niederlein 366* (BA); Ayo. Uruguaí, km 10, 14 ene. 1963, *Partridge s.n.* (BA 61693); Oberá, 24 dic. 1970, *Mroginski 80* (CTES); San Ignacio, km 101, 20 dic. 1945, *Schwarz 1699* (CTES); San Ignacio, 11 dic. 1941, *Biraben 5324* (LP); Salto Tabay, 14 oct. 1977, *Cabrera et al. 28771* (SI); San Javier, S. Javier, nov. 1962, *Martínez Crovetto 9764* (SI), 8 dic. 1945, *Bertoni 2494* (CTES), 26 ene. 1976, *Krapovickas et al. 28905* (CTES, SI); Acaraguá, 19 nov. 1946, *Bertoni 3073* (CTES). **San Pedro:** Monte Carlo, 2 mayo 1951, *Montes 15207* (CTES); Parque Prov. Moconá, 23 abr. 1993, *Rodríguez et al. 557* (CTES). **Corrientes:** Santo Tomé, Ea. Timbó, 8 dic. 1981, *Tressens et al. 1598* (CTES).

A *Galianthe hispidula* se la reconoce fácilmente por ser esta una hierba sufruticosa, estolonífera, de tallos simples. Común en sotobosque.

Figura 7. *Galianthe hispidula*. —A. Planta. —B. Corte transversal del tallo. —C. Vaina estipular. —D, E. Flor brevistila. —F, G. Flor longistila. —H. Fruto. —I. Semilla, cara ventral. —J. Corte transversal de semilla. A–C, F–J, *Martínez Crovetto et al. 5777*; D, E, *Martínez Crovetto et al. 5834*.

7. **Galianthe humilis** E. L. Cabral & Bacigalupo, sp. nov. TIPO: Brasil. Minas Gerais: Pouso Alegre, 2 mayo 1927, *F. C. Hoehne 19357* (holótipo, SP). Figura 8.

Suffrutex caulibus tetragonis, glabris, anguste alatis, alis glabris vel scabriusculis. Folia sessilia 25–45 mm longa, 7–9 mm lata, elliptica, apice acuto, base attenuata, nervis secundariis 3–4 partibus, conspicuis, supra glabra vel scabriuscula. Vagina folii 3 mm longa aliqui pilosa,

Figura 8. *Galianthe humilis.* —A. Rama. —B–D. Flor longistila. —E. Fruto. A–D, *Souza León 11*; E, *Hoehne 19357.*

3–7 laciniata. Flores in cymis compositis dispositi. Calyx tetrasectus, 1.2–2 mm longus, cum 2 segmentis leviter majoribus, glabris vel margine scabriusculo. Hypanthium glabrum, 1.8 mm longum. Corolla alba, 4-partita, 3.6 mm longa, cum lobulis tubus corollinus aequantibus, intus dense pubescentibus. Flos longistylus corolla 3.6 mm longa, antheris 1 mm longis, stylo 2 mm longo, ramis stigmatibus 0.6 mm longis. Flos brevistilus ignotus. Fructus 5 mm longus, subturbinatus, lateraliter aliquantum compressus, glaber, reticulato-foveolatus in sicco. Semen immaturum 3 mm longum, reticulato-foveolatum, strophiolo faciem ventralem in parte tegente.

Hierba sufruticosa de tallos tetrágonos, glabros, con alas angostas, glabras o escabriúsculas. Hojas sésiles, de 25–45 × 7–9 mm, elípticas, de ápice agudo y base atenuada con 3–4 pares de nervios secundarios, marcados en la haz y en resalto en el envés, glabras o algo escabriúsculas en la haz sobre todo hacia el margen, éste recurvado. Vaina estipular 3 mm de long., algo pilosa con 3–7 lacinias glabras, hasta de 4 mm long. Inflorescencia cimoidal con inflorescencias parciales fasciculadas, par-

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Figura 9. *Galianthe polygonoides.* —A. Rama. —B. Vaina estipular. —C, D. Flor brevistila. —E, F. Flor longistila. —G. Fruto. —H. Semilla no madura, cara ventral. A–D, G, H, *Braga 1741*; E, F, *Sucre 4190.*

2 cm
2 mm
B
A
C
1 mm
D
E
F
1 mm
H
1 mm
G

2 cm
A
2 mm
B
1 mm
C
E
1 mm
D
LG·95
F

vifloras hasta flores solitarias en algunos nudos. Cáliz 4-partido, 1.2–2 mm long., de segmentos triangulares, 2 ligeramente mayores, con algún dientecito en los senos intercalares, glabros o de borde escabriúsculo. Hipanto glabro, subturbinado, 1.8 mm long. Corola blanca, 4-lobada, 3.6 mm long. de lóbulos tan largos como el tubo corolino, con densa pubescencia en su interior. Flor longistila: corola 3.6 mm long., anteras 1 mm long., estilo 2 mm long., ramas del estigma de 0.6 mm de largo. Flor brevistila: no vista. Fruto 5 mm long., subturbinado, algo comprimido lateralmente, glabro, oscuramente reticulado-foveolado al secarse. Semilla inmadura, 3 mm long., reticulado-foveolada con estrofíolo cubriendo parcialmente la cara ventral.

Distribución (Fig. 11). Se ha coleccionado hasta el momento sólo en Brasil, en el Estado de Minas Gerais, en campos altos, de suelos rocosos.

Material examinado. BRASIL. **Minas Gerais:** Carangola, 1400 m s.m., 20°43′S, 42°29′W, 22 jul. 1988, *L. Souza Leon 11* (SPF); sin localidad, 1858, *Weddell s.n.* (G).

Se asemeja a *Galianthe cymosa,* siendo ésta más grácil, de tallos finos, minutamente papilosos, con inflorescencias parciales densas y corolas de lóbulos más cortos que el tubo.

8. Galianthe polygonoides E. L. Cabral & Bacigalupo, sp. nov. TIPO: Brasil. Rio de Janeiro: Petrópolis, Vale do Bonsucesso, 750 m s.m., 15 nov. 1969, *D. L. S. Braga 1741* (holótipo, RB; isótipo, CTES). Figura 9.

Suffrutex scandens, caulibus fistulosis, glabris, ramis brevibus paucibus vel absentibus. Folia elliptica ad lanceolata 40–60 × 10–14 mm, glabra, margine revoluto scabriusculo. Vagina stipularis glabra conspicuissima 7–13 mm de largo, 6–7 laciniis, inaequalibus 1–5 mm de largo. Inflorescentia thyrsoidea (monochasia, dichasia, vel pleochasia); inflorescentiis partialibus cymosis contractis, fasciculatis, interse distinctis (cincinndeis) hypanthio scabriusculo 1.5–2 mm de largo, calyx tetrasectus, segmentis triangularibus-subulatis. Corolla alba externe micropapillata, lobi dorso apicale dense papilloso, intus medium annulari pilis moniliformis, disco bipartito papilloso. Flores dimorfi. Fructus scabriusculus 2–2.5 mm, 2 mericarpis indehiscentibus, sepala persistente. Semina ± plana-convexa, strophiolo faciem ventralem in parte in linea media tegente.

Sufrútice trepador, tallos fistulosos, subcilíndricos a tetrágonos, glabros, entrenudos de 6–9 cm de largo, brotes axilares escasos a nulos. Hojas de 40–60 × 10–14 mm, elípticas a lanceoladas, de ápice agudo a acuminado y base atenuada en breve pseudopecíolo, glabras, con bordes revolutos, escabriúsculos, levemente discoloras, con 3–4 pares de venas secundarias subopuestas. Vaina estipular muy conspicua, tubulosa, glabra, 7–13 mm long., con 6–7 lacinias. Inflorescencia cimoidal (monocasial, dicasial o pleocasial), con paracladios cincinoides. Cáliz con 4 segmentos triangular-subulados de 1.5–2.5 mm long., escabriúsculos, a veces con dientes intercalares; hipanto obcónico, escabriúsculo, 1.5–2 mm long. Corola blanca, externamente micropapilada, con papilas más densas y más grandes en el dorso apical de los lóbulos; superficie interna, con pelos moniliformes sobre el tubo hasta la base de los lóbulos; disco bipartido papiloso. Flor brevistila: corola 3–3.2 mm long., lóbulos iguales o más cortos que el tubo corolino; filamentos estaminales 1–1.5 mm long., anteras 1 mm long., estilo 2–3 mm long., bifurcado en su extremo. Flor longistila: corola 3–3.5 mm long., lóbulos más cortos que el tubo corolino, filamentos estaminales muy breves y anteras 0.7–1 mm, estilo 3.5–4 mm long., ramas estilares filiformes 1 mm, densamente papilosas. Fruto subturbinado, escabriúsculo, 2–2.5 mm long., separándose en dos mericarpos indehiscentes, sépalos persistentes. Semilla más o menos plano-convexa, 1.7–2 mm long., cara ventral cubierta parcialmente por el estrofíolo en la línea media, cara dorsal foveolada.

Distribución (Fig. 11). Esta especie fue encontrada hasta el presente, sólo en Brasil, en el Estado de Rio de Janeiro, Petrópolis a 750–800 m s.m.

Material examinado. BRASIL. **Rio de Janeiro:** Petrópolis, 24 nov. 1968, *D. Sucre et al. 4190* (RB); Caetetu, 1 jul. 1943, *G. Goés et al. 240* (RB); Carangola, 29 ago. 1943, *G. Goés et al. 500* (RB); Grota do Jacó, 800 m s.m., 2 nov. 1968, *D. Sucre et al. 4013* (US), 2 dic. 1971, *J. Barcía 349* (R); Araras, Ma. Comprida, 30 ene. 1971, *Urbano 9927* (K); Serra da Estrella, 1844, *Weddell 44* (P).

Galianthe polygonoides se individualiza por su hábito trepador y por la vaina estipular muy notable, tubulosa por encima de la inserción de las hojas, a modo de una ocrea, similar a la que presenta *G. vaginata* de la que se distingue por tener esta vainas pubescentes y tallo marcadamente alado.

9. Galianthe vaginata E. L. Cabral & Bacigalupo, sp. nov. TIPO: Brasil. Minas Gerais: Sierra do Itatiaia, ad marginem viae, ca. 1800 m s.m., 25 mayo 1902, *P. Dusén 109* (holótipo, R). Figura 10.

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Figura 10. *Galianthe vaginata.* —A. Rama. —B. Vaina estipular. —C. Botón. —D–F. Flor longistila. A–F, *Dusén 109.*

Figura 11. Mapa de distribución de las especies de *Galianthe* subg. *Ebelia*.

Suffrutex erectus, caulibus tetragonis conspicue alatis. Folia 30–90 mm longa, 10–24 mm lata, discoloria, elliptica, apice acuto vel acuminato, base attenuata, nervis secundariis 4–5 paribus, supra glabra vel minute papillosa, subtus scabriuscula plerumque in nervis et marginibus. Vagina stipularis tubulosa, supra paribus foliorum suum prolongata, 6–12 mm longa, pubescentia, margine laciniata. Inflorescentiae cymoides, 1(2–3) verticillatae cum inflorescentiis partialibus fasciculatis, laxis. Flores dimorphi, hypantho turbinato, scabriusculo. Flos longistylus calice cum 4 segmentis deltoideo-subulatis: duobus 1.5–2 mm longis alterni cum duobus aliquod minoribus. Corolla alba, 4.5–4.7 mm longa, lobulis quam tubo brevioribus; tubo corollino usque lobulorum dimidiam partem disperse piloso. Antherae 1–1.2 mm longae cum filamentis brevissimis. Stylus 3.5–4.5 mm longus, ramis 0.8–1 mm longis. Flos brevistylus et fructus haud visus.

Sufrútice de tallos tetrágonos notoriamente alados. Hojas de 30–90 × 10–24 mm, discoloras, elípticas, de ápice agudo o acuminado y base atenuada, con 4–5 pares de nervios secundarios, haz glabra con diminutas papilas sobre los nervios, envés escabriúsculo esencialmente sobre los nervios y los bordes; vaina estipular tubulosa, prolongada por encima del par de hojas correspondiente, 6–12 mm de largo, pubescente, de bordes laciniados. Inflorescencia cimoidal con inflorescencias parciales fasciculadas, distanciadas entre sí. Flores heterostilas, hipanto turbinado, escabriúsculo. Flor longistila: cáliz de 4 segmentos triangular-subulados, 2 de 1.5–2 mm long. alternados con 2 ligeramente menores. Corola blanca, 4.5–4.7 mm long., de lóbulos más cortos que el tubo, con pelos dispersos en el interior del tubo corolino hasta la mitad de los lóbulos. Anteras 1–1.2 mm long., filamentos muy breves. Estilo 3.5–4.5 mm long., ramas estilares de 0.8–1 mm long. Flor brevistila y frutos no vistos.

Distribución (Fig. 11). Esta especie es brasileña y habita en los Estados de Minas Gerais y São Paulo.

Material examinado. BRASIL. **São Paulo:** Campos do Jordão, in campestris dumetosis, ene. 1944, *E. Frider-*

ich S. J. s.n. (PACA 27764). **Minas Gerais:** prov. Minarum Ad Caldas, 1867, *A. Regnell I: 178* (BR).

ESPECIES DUDOSAS

Triodon polymorphus var. *intermedius* DC., Prodr. 4: 566. 1830. In Brasil meridionali, Sellow. TIPO: B, destruido. Probablemente existan duplicados no localizados. Su autor la caracteriza por sus hojas de tamaño intermedio.

Diodia polymorpha var. *floribunda* K. Schum., in Mart., Fl. Bras. 6(6): 13. 1888. TIPO: no designado, Brasil. Los ejemplares citados: "in provincia Rio de Janeiro prope Canta Gallo: Peckolt; Glaziou 3028; in silvis prope Gongo Soco: Bunbury; loco haud accuratius indicato: Sello 3433" B, destruidos. Duplicados no localizados. Según su autor se corresponde con plantas de hojas pequeñas, 5–13 × 1–4 mm, cáliz 2-mero.

Diodia polymorpha var. *lasiodisca* K. Schum., in Mart., Fl. Bras. 6(6): 12. 1888. TIPO: Brasil. "Habitä in provincia Minas Geraes prope Sumidorio: de Langsdorff" (holótipo, B destruido). No se han localizado duplicados.

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GÉNERO *GALIANTHE* SUBG. *EBELIA* (RUBIACEAE: SPERMACOCEAE): ESTUDIO PALINOLÓGICO[1]

Stella Maris Pire[2]

Resumen

Se estudia el polen de las especies de la tribu Spermacoceae conocidas actualmente como: *Borreria anthospermoides* DC., *Diodia brasiliensis* Spreng., *D. cymosa* Cham., *D. hispidula* A. Rich. ex DC., *Knoxia dichotoma* Willd. ex Roem. & Schult. y *D. brasiliensis* var. *angulata* (Benth.) Standl., y se señala su afinidad con el polen del género *Galianthe* Griseb. Este estudio palinológico refuerza el criterio sustentado por Cabral y Bacigalupo de ampliar los límites del género *Galianthe* e incluir estas especies en el nuevo subgénero *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, junto con *G. dichasia* (Sucre & C. G. Costa) E. L. Cabral, *G. humilis* E. L. Cabral & Bacigalupo y *G. polygonoides* E. L. Cabral & Bacigalupo, por sus frutos de mericarpos indehiscentes.

Abstract

The pollen of the species of tribe Spermacoceae currently known as *Borreria anthospermoides* DC., *Diodia brasiliensis* Spreng., *D. cymosa* Cham., *D. hispidula* A. Rich. ex DC., *D. dichotoma* (Willd. ex Roem. & Schult.) K. Schum., and *D. brasiliensis* var. *angulata* (Benth.) Standl. is studied, and its affinity with the pollen of the genus *Galianthe* Griseb. is indicated. This palynological study reinforces the suggestion of Cabral and Bacigalupo to extend the boundaries of the genus *Galianthe* to include the species listed above, because of their fruits with indehiscent mericarps, in the new *Galianthe* subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo, together with *G. dichasia* (Sucre & C. G. Costa) E. L. Cabral, *G. humilis* E. L. Cabral & Bacigalupo, and *G. polygonoides* E. L. Cabral & Bacigalupo.

Este trabajo es parte de un proyecto más amplio que comprende el estudio palinológico de toda la tribu Spermacoceae. Esta es una de las tribus de Rubiaceae que incluye varios géneros conflictivos o críticos cuya delimitación es discutida, como *Spermacoce* L., *Diodia* L., *Borreria* G. F. W. Meyer, etc. (Steyermark, 1974; Verdcourt, 1976; Fosberg et al., 1981; Howard, 1989; Burger & Taylor, 1993, entre otros). El estudio palinológico pretende aportar datos que ayuden a la redefinición de los géneros, emprendimiento encarado junto con N. Bacigalupo y E. Cabral.

Hasta el momento se ha estudiado el polen de 145 especies representantes de la totalidad de los géneros (16) de las Spermacoceae citadas para América. Al realizar este estudio se encontró que algunas especies del género *Diodia* L. poseen granos de polen con retículo complejo, ésto es con un suprarretículo y un infrarretículo a un nivel más bajo que el anterior. En Rubiáceas, este tipo de ornamentación, hasta el momento, sólo ha sido descripto para *Galianthe* Griseb. (Pire & Cabral, 1992). Este género ha sido recientemente revalidado por Cabral (1991).

Diodia, en sentido amplio, es un género que incluye taxones de caracteres muy dispares que no se corresponden con su definición genérica. Estos caracteres involucran al fruto, inflorescencia, morfología floral y también al polen. Bacigalupo y Cabral (inédito) reconocen, hasta el momento, 4 especies como válidas de *Diodia* (*D. virginiana* L., *D. kuntzei* K. Schum., *D. macrophylla* K. Schum. y *D. saponariifolia* Cham. & Schldl.), principalmente por presentar frutos indehiscentes, y proponen la reubicación de las restantes especies en otros géneros. El primer paso para la reubicación de las

[1] Esta communicación constituye una parte del trabajo "Palynology of the Tribe Spermacoceae (Rubiaceae)," presentado durante la International Conference on the Systematics of the Rubiaceae (1993), en St. Louis, Missouri. Expreso mi agradecimiento a las siguientes personas que me brindaron el material de estudio y aportaron valiosas sugerencias: E. Cabral, N. Bacigalupo (además, la lectura crítica del manuscrito) y R. Herbst. A las instituciones que otorgaron el apoyo financiero para este estudio: Universidad Nacional del Nordeste y CONICET. Mi reconocimiento, también para los directivos del IBONE por facilitarme el uso del Herbario y Biblioteca; lo hago extensivo a los curadores de los herbarios mencionadas en este trabajo.

[2] Facultad de Ciencias Exactas y Naturales y Agrimensura (U.N.N.E.)–PRINGEPA, C.C. 128, 3400-Corrientes, Argentina.

Cuadro 1. Combinaciones nuevas propuestas por Cabral y Bacigalupo (1997) con sus nombres actuales equivalentes.

Nombres actuales	Combinaciones nuevas
Borreria anthospermoides DC.	*Galianthe bogotensis* (Kunth) E. L. Cabral & Bacigalupo
Borreria dichasia Sucre & C. G. Costa	*Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral
Diodia brasiliensis Spreng.	*Galianthe brasiliensis* (Spreng.) E. L. Cabral & Bacigalupo
Diodia brasiliensis var. *angulata* (Benth.) Standl.	*Galianthe brasiliensis* subsp. *angulata* (Benth.) E. L. Cabral & Bacigalupo
Diodia cymosa Cham.	*Galianthe cymosa* (Cham.) E. L. Cabral & Bacigalupo
Knoxia dichotoma Willd. ex Roem. & Schult.	*Galianthe dichotoma* (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo
Diodia hispidula A. Rich. ex DC.	*Galianthe hispidula* (A. Rich. ex DC.) E. L. Cabral & Bacigalupo
—	*Galianthe humilis* E. L. Cabral & Bacigalupo
—	*Galianthe polygonoides* E. L. Cabral & Bacigalupo
—	*Galianthe vaginata* E. L. Cabral & Bacigalupo

especies lo constituye la inclusión de *Diodia brasiliensis* Spreng., *D. cymosa* Cham., *D. hispidula* A. Rich. ex DC., *Knoxia dichotoma* Willd. ex Roem. & Schult., *Diodia brasiliensis* var. *angulata* (Benth.) Standl., en *Galianthe* (Cabral & Bacigalupo, 1997, en este volumen). Al mismo tiempo se incorpora *Borreria anthospermoides* DC.; todas estas especies poseen, como *Galianthe*, frutos dehiscentes, flores heterostilas o dimorfas e inflorescencias casi siempre complejas, tirsoides o cimoidales, con inflorescencias parciales en dicasios más o menos congestos. Si bien, a diferencia de *Galianthe* que posee frutos con mericarpios dehiscentes, los mericarpios de estas especies son indehiscentes. Por esta razón se las ha agrupado en un nuevo subgénero: *G.* subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo (1997). Dentro de este subgénero estan comprendidas además, *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, *G. humilis* E. L. Cabral & Bacigalupo, *G. polygonoides* E. L. Cabral & Bacigalupo y *G. vaginata* E. L. Cabral & Bacigalupo.

En el Cuadro 1 se da las equivalencias entre los nombres conocidos y las combinaciones nuevas propuestas por Cabral y Bacigalupo, de las especies comprendidas en *Galianthe* subg. *Ebelia*.

Antecedentes

De este grupo de especies son pocas las que han sido estudiadas anteriormente desde el punto de vista palinológico. Galati en su Tesis Doctoral (Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, 1988, inédito), al estudiar la embriología de la tribu Spermacoceae, analiza el polen de 7 géneros y 19 especies, entre ellas *Diodia brasiliensis* y ya señala la coincidencia de caracteres palinológicos y embriológicos entre esta especie y otras dos, *Borreria fastigiata* (Griseb.) K. Schum. y *B. laxa* Cham. & Schldl., que ahora se consideran dentro de *Galianthe* (Cabral, 1991). Esta coincidencia se refleja también, en la tipología del megagametófito (Galati, 1991).

En un trabajo anterior (Pire & Cabral, 1992), al analizar el valor del polen en la revalidación del género *Galianthe*, se hace referencia a la morfología polínica de *G. dichasia* y de *Borreria anthospermoides*. Esta última especie no fue incorporada dentro de *Galianthe* por Cabral (1991), por presentar frutos con mericarpos indehiscentes y granos de polen con retículo simple, quedando pendiente, en ese momento, su clasificación genérica. A *Borreria dichasia* Sucre & C. G. Costa se la incorporó como *Galianthe dichasia* (Sucre & C. G. Costa) E. L. Cabral, a pesar de sus frutos de mericarpos indehiscentes, porque en ese momento no se disponía de material fructificado y el resto de los caracteres coincidían bien con *Galianthe*.

Material y Métodos

Para el estudio de los granos de polen se utilizó anteras de botones florales bien desarrollados, obtenidos de material de herbario. Los ejemplares testigos se encuentran depositados en los siguientes Herbarios: CTES, MBM, MO, NY, SI, SP y RB.

El material palinológico, para su observación con microscopio óptico, fue tratado de acuerdo a la técnica de acetólisis de Erdtman (1966), utilizándose gelatina-glicerinada como medio de montaje. Dichos preparados se hallan depositados en la Palinoteca de la Universidad Nacional del Nordeste (PAL-CTES). Para la observación con microscopio electrónico de barrido (MEB) se utilizó polen acetolizado y en algunos casos polen natural, en ambos

casos se los lavó varias veces con agua destilada y se los montó en un trocito de "papel España."

De cada especie se estudió el polen de flores longistilas y brevistilas. Sobre un mínimo de 30 granos, se midieron los parámetros: eje polar y diámetro ecuatorial; en un menor número de granos se midieron: el espesor de la exina, largo y ancho de los colpos, diámetros mayor y menor de las endoaperturas, distancia entre colpos. Además se calculó la relación entre longitud del colpo o ectoapertura (ECA) y longitud del grano o eje polar (P) y se clasificó los colpos en: cortos (ECA/P = 0.20–0.35), medianos (ECA/P = 0.36–0.45) y largos (ECA/P = 0.46–0.65). Estas observaciones se efectuaron utilizando un microscopio óptico Leitz Orthomat. Otras mediciones como, ancho de los muros del retículo, diámetro de los lúmenes, largo y ancho de las espínulas, se realizaron sobre la base de fotomicrografías tomadas con el microscopio electrónico de barrido JEOL-JSMT 100 del Servicio de Microscopía Electrónica de la Facultad de Ciencias Naturales y Museo de la Universidad Nacional de La Plata.

La terminología utilizada es básicamente la de Erdtman (1966) y se consultó también Kremp (1968).

A continuación se cita el material examinado bajo el nombre de la nueva combinación propuesta por Cabral y Bacigalupo y entre barras el basónimo correspondiente.

MATERIAL EXAMINADO

Galianthe bogotensis (Kunth) E. L. Cabral & Bacigalupo [*Borreria anthospermoides* DC.]. Flores brevistilas: COLOMBIA. **Boyacá:** Socha, *Fosberg 22225* (NY) [PAL-CTES 3792]. NUEVA GRANADA. *J. J. Triana 75* (NY) [PAL-CTES 3952]. Flores longistilas: COLOMBIA. **Boyacá:** Cord. Oriental, Páramo de Belén, *H. Barclay & P. Juajibioy 7661* (MO) [PAL-CTES 3120]. **Cundinamarca:** Cordillera Oriental, Páramo, *H. García Barriga 16136* (NY) [PAL-CTES 3790].

Galianthe brasiliensis (Spreng.) E. L. Cabral & Bacigalupo [*Diodia brasiliensis* Spreng.]. Flores brevistilas: PARAGUAY. Encarnación, Mboy-caé, *Bertoni 2401* (CTES) [PAL-CTES 3175]. Flores longistilas: ARGENTINA. **Misiones:** Candelaria, Cerro Corá, *Bertoni 2604* (CTES) [PAL-CTES 3174].

Galianthe brasiliensis subsp. *angulata* (Benth.) E. L. Cabral & Bacigalupo [*Triodon angulatum* Benth.]. Flores brevistilas: MEXICO. **Veracruz:** Jicó, *Pringle 10803* (CTES) [PAL-CTES 3404]. Flores longistilas: MEXICO. **Hidalgo:** El Candeje, *Gimate 852* (CTES) [PAL-CTES 3789].

Galianthe cymosa (Cham.) E. L. Cabral & Bacigalupo [*Diodia cymosa* Cham.]. Flores brevistilas: BRASIL. **Paraná:** Curitiba, Barigui, *Ferreira 186* (MO) [PAL-CTES 3794].

Galianthe dichasia (Sucre & C. G. Costa) E. L. Cabral [*Borreria dichasia* Sucre & C. G. Costa]. Flores brevistilas: BRASIL. **Paraná:** Curitiba, *Tessmann 67* (MBM) [PAL-CTES 3077]. Flores longistilas: BRASIL. **Paraná:** Rinçao, *Hatschbach 624* (SP) [PAL-CTES 3076].

Galianthe dichotoma (Willd. ex Roem. & Schult.) E. L. Cabral & Bacigalupo [*Knoxia dichotoma* Willd. ex Roem. & Schult.]. Flores brevistilas: ECUADOR. **Azuay–Loja:** Nudo de Cordillera Occidental y Cord. Oriental, entre Oña y Rancho Ovejero, *Barclay et al. 8454* (MO) [PAL-CTES 3114]. Flores longistilas: ECUADOR. **Pichincha:** Cantón Quito, *C. Cerón 2253* (MO) [PAL-CTES 3953]. PERU. **Cajamarca:** camino a laguna Chamis, *Sánchez Vega 759* (SI) [PAL-CTES 3407].

Galianthe hispidula (A. Rich. ex DC.) E. L. Cabral & Bacigalupo [*Diodia hispidula* A. Rich. ex DC.]. Flores brevistilas: ARGENTINA. **Misiones:** L. N. Alem, *Cabral et al. 496* (CTES) [PAL-CTES 3393]. Flores longistilas: ARGENTINA. **Corrientes:** Santo Tomé, Ea.Timbó, *Tressens et al. 1598* (CTES) [PAL-CTES 3787]. **Misiones:** San Ignacio, *Schwarz 1699* (CTES) [PAL-CTES 3954].

Galianthe humilis E. L. Cabral & Bacigalupo. Flores longistilas: BRASIL. **Minas Gerais:** Pouso Alegre, *Hoehne 19357* (SP) [PAL-CTES 3392].

Galianthe polygonoides E. L. Cabral & Bacigalupo. Flores brevistilas: BRASIL. **Rio de Janeiro:** Petrópolis, Caetetú, *D. C. Goés et al. 240* (RB) [PAL-CTES 3788]; Carangola, *Goés et al. 500* (RB) [PAL-CTES 3955]. Flores longistilas: BRASIL. **Rio de Janeiro:** Petropolis, *Sucre 4190 et al.* (RB) [PAL-CTES 3391].

DESCRIPCIÓN GENERAL DE LOS GRANOS DE POLEN

Las especies de *Galianthe* subg. *Ebelia* constituyen un grupo bastante homogéneo desde el punto de vista palinológico. Los granos de polen presentan las siguientes características: isopolares, radiosimétricos, tamaño mediano (25–50 μm), oblato-esferoidales o prolato-esferoidales. De acuerdo a las aperturas son zono-colporados: 6–7 colporados en *Galianthe brasiliensis* y *Galianthe dichasia* (flores brevistilas) y 8–9(–10) colporados en el resto de las especies. Los colpos generalmente son largos y las endoaperturas lalongadas. La exina, de 2.5–3.5 μm de espesor, es semitectada-reticulada, con retículo complejo diferenciado en un suprarretículo (SR), psilado, y un infrarretículo (IR), espinulado, a un nivel más bajo que el anterior. Se exceptúan *G. bogotensis* y *G. dichotoma* que presentan retículo simple, de muros espinulados.

El SR puede presentar mallas cerradas o abiertas (con muros interrumpidos), que, generalmente, aumentan de tamaño hacia los polos.

El IR se puede encontrar distintamente diferenciado; por lo general, se lo observa como puentes, simples o ramificados, que atraviezan los lúmenes del SR (1), o a veces, reducido a espínulas ubicadas lateralmente en la base de los muros del SR (*G. brasiliensis* y *G. humilis*) (2), o bien, está totalmente ausente y en este caso las espínulas se localizan sobre el SR (*G. dichotoma* y *G. bogotensis*) (3). De este modo, se podrían reconocer 3 estadíos

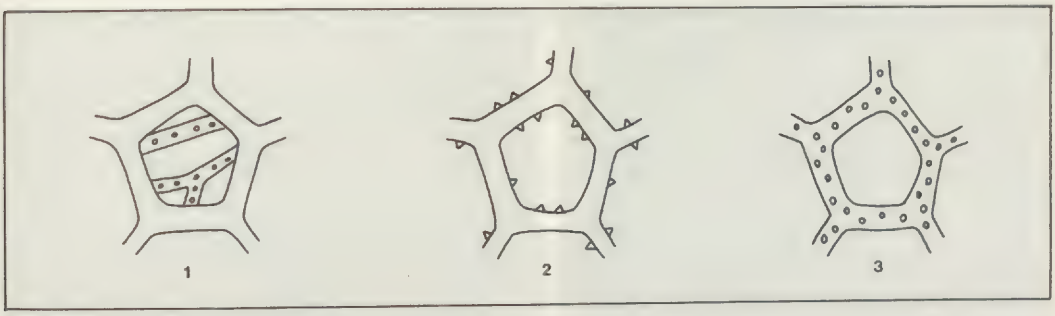


Figura 1. Representación gráfica de los estadíos de modificación de la exina entre retículo complejo (1–2) y retículo simple (3).

de modificación de la estructura de la exina, entre retículo complejo y retículo simple (Fig. 1), cuya secuencia evolutiva no puede ser establecida aún con certeza.

Por otra parte, las flores longistilas y brevistilas presentan un dimorfismo polínico poco marcado que está dado por finas diferencias en la ornamentación de la exina y por un tamaño levemente mayor de los granos de polen en flores brevistilas.

Diferencias entre las Especies

Las principales diferencias entre las especies estan dadas por:

(1) ornamentación de la exina

De acuerdo a ella se pueden agrupar las especies en: con retículo simple o con retículo complejo.

Con retículo simple hay 2 especies: *G. bogotensis* y *G. dichotoma,* que presentan diferencias entre sí. En la primera el retículo posee lúmenes profundos y amplios (de hasta 4.5 μm de ancho), entre los que se intercalan otros menores (0.2 μm) y muros rectilíneos o suavemente curvilíneos, provistos de 1 sola hilera de espínulas (Fig. 2A, C). En la segunda especie, los lúmenes son comprimidos, de contorno muy irregular y de menor tamaño (de 2–3 μm, a veces 3.5 μm de largo × 0.6–1 μm de ancho), los muros son curvilíneos con 1 ó 2 hileras de espínulas (Fig. 2B, D).

Con respecto al retículo complejo, las variantes observadas corresponden a los 3 tipos básicos ya descriptos para otras especies de *Galianthe* (Pire & Cabral, 1992):

TIPO I: SR completo en todo el grano; IR poco visible;

TIPO II: SR interrumpido formando mallas abiertas en los mesocolpios; IR parcialmente visible;

TIPO III: SR reducido a fragmentos pequeños en la zona ecuatorial; IR parcial a completamente visible.

El TIPO I es el más frecuente, el TIPO II se presenta en *G. brasiliensis* subsp. *angulata* y en *G. cymosa* (Fig. 3A–D) y el TIPO III, sólo en flores brevistilas de *G. polygonoides* (Fig. 3E–G). En el TIPO I los muros del SR son ± rectilíneos y los lúmenes poligonales, isodiamétricos o alargados. En los TIPOS II y III, los muros son curvilíneos y los lúmenes tienen forma irregular. Con respecto al IR en algunas especies se observaron variaciones en la distribución de las espínulas: en *G. brasiliensis* subsp. *angulata* (flor brevistila) los muros son pobremente espinulados; en mesocolpios poseen 1 ó 2 espínulas y hacia los polos tienden a ser psilados (Fig. 3C); en *G. brasiliensis,* y flores longistilas de *G. humilis,* y *G. polygonoides,* las espínulas se localizan, ya sea sobre los muros que atraviezan los lúmenes de SR o ya sea lateralmente en la base del SR (Figs. 2G, 3E–G, 4).

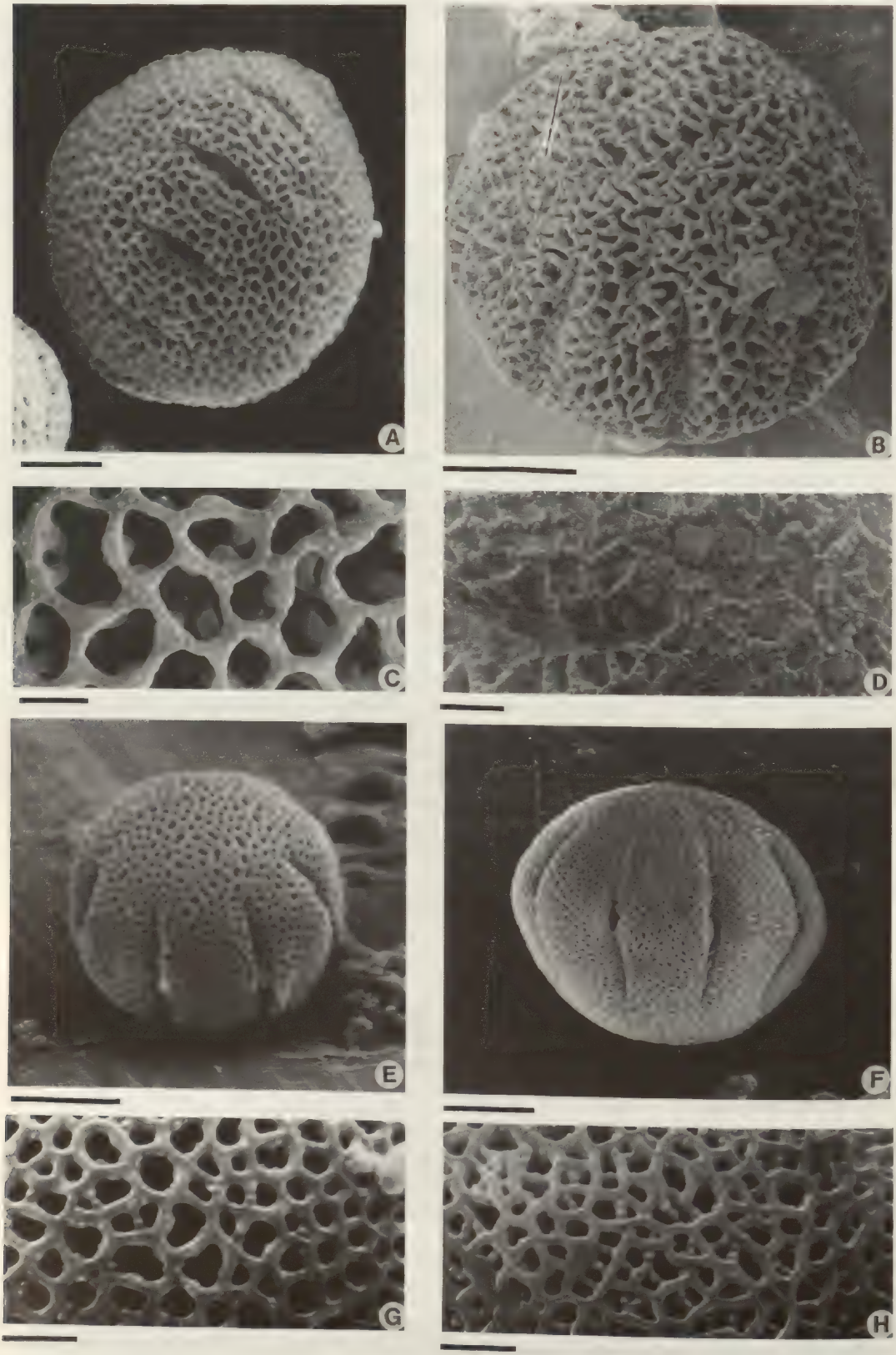
(2) longitud del colpo o ectoapertura

En todas las especies, excepto *G. bogotensis,* los granos de polen poseen colpos largos (ECA/P mayor de 0.45). Sin embargo, algunas especies, como *G. dichotoma* y las flores longistilas de *G. brasiliensis* subsp. *angulata* y *G. dichasia,* pueden tener, además, granos con colpos medianos (ECA/P = 0.40–0.51). En *G. bogotensis* los colpos pueden ser cortos o medianos (ECA/P = 0.33–0.43).

Otras diferencias respecto al número de aperturas, forma y tamaño de los granos, diámetro de los lúmenes del SR y ancho de los muros del SR e IR, se exponen en el Cuadro 2.

Discusión y Conclusiones

En el Figura 5 se resumen, en forma esquemática, los caracteres exomorfológicos y caracteres palinológicos de los géneros *Galianthe* (subg. *Ebe-*


A
B
C
D
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G
H

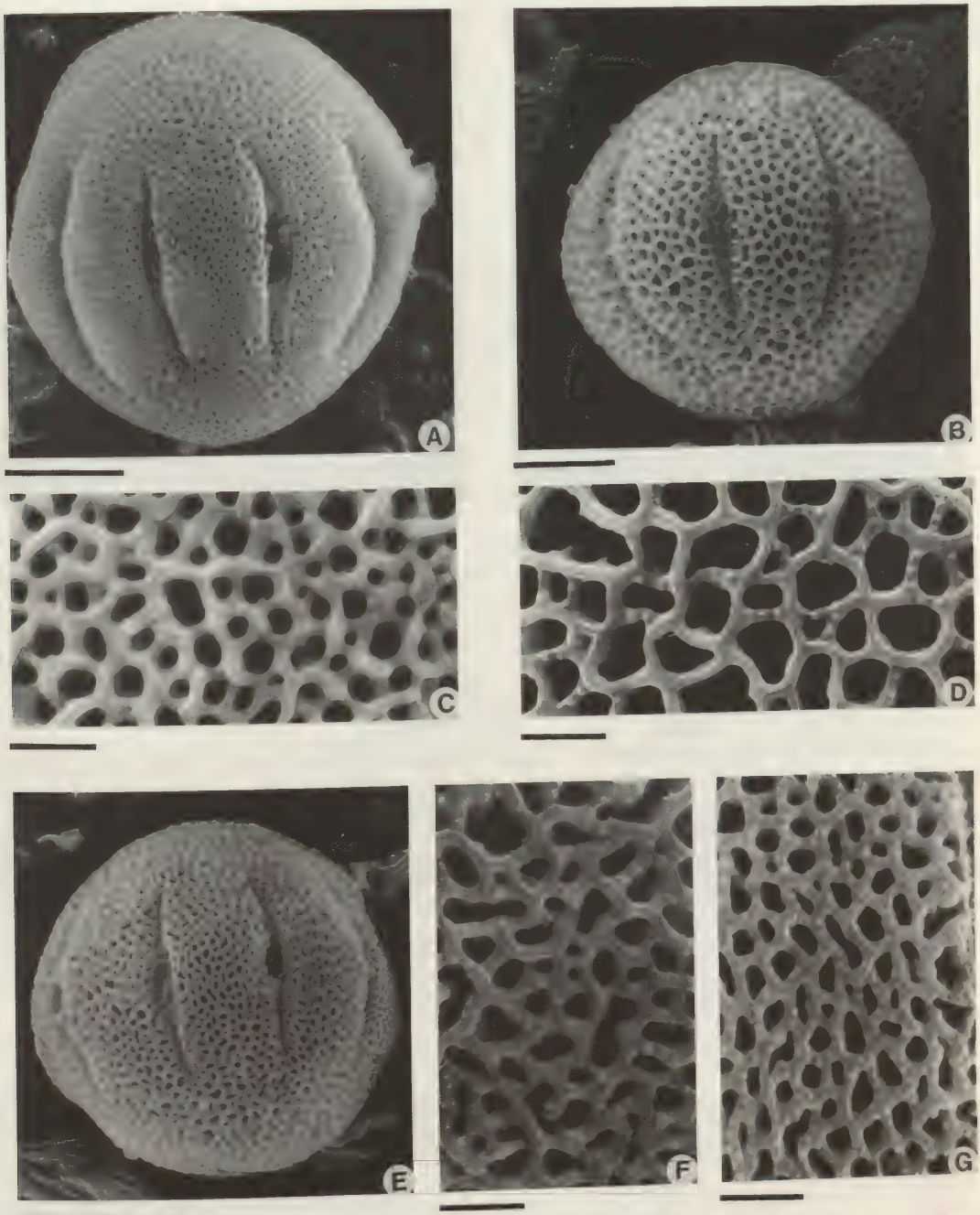

Figura 3. Granos en vista ecuatorial y detalle de la escultura del apocolpio. —A, C. *Galianthe brasiliensis* subsp. *angulata*, f.b. (*Pringle 10803*). —B, D. *G. cymosa*, f.b. (*Ferreira 186*). E–G. *G. polygonoides*, f.b. —F. Apocolpio. —G. Mesocolpio (*Goés et al. 240*). Las escalas equivalen a 10 μm en A, B, E y 2 μm en C, D, F, G. (f.b., flor brevistila; f.l., flor longistila.)

←

Figura 2. Granos en vista ecuatorial y detalle de la escultura del apocolpio. —A, C. *Galianthe bogotensis*, f.b. (*Fosberg 22225*). —B, D. *G. dichotoma*, f.l. (*Sanchez Vega 759*). E, G. *G. brasiliensis*. —E. f.b. (*Bertoni 2401*). —G. (*Fosberg 22225*). —B, D. *G. dichotoma*, f.l. (*Sanchez Vega 759*). E, G. *G. brasiliensis*. —E. f.b. (*Bertoni 2401*). —G. f.l. (*Bertoni 2604*). —F, H. *G. hispidula*, f.l. (*Tressens et al. 1598*). Las escalas equivalen a 10 μm en A, B, E, F y a 2 μm en C, D, G, H. (f.b., flor brevistila; f.l., flor longistila.)

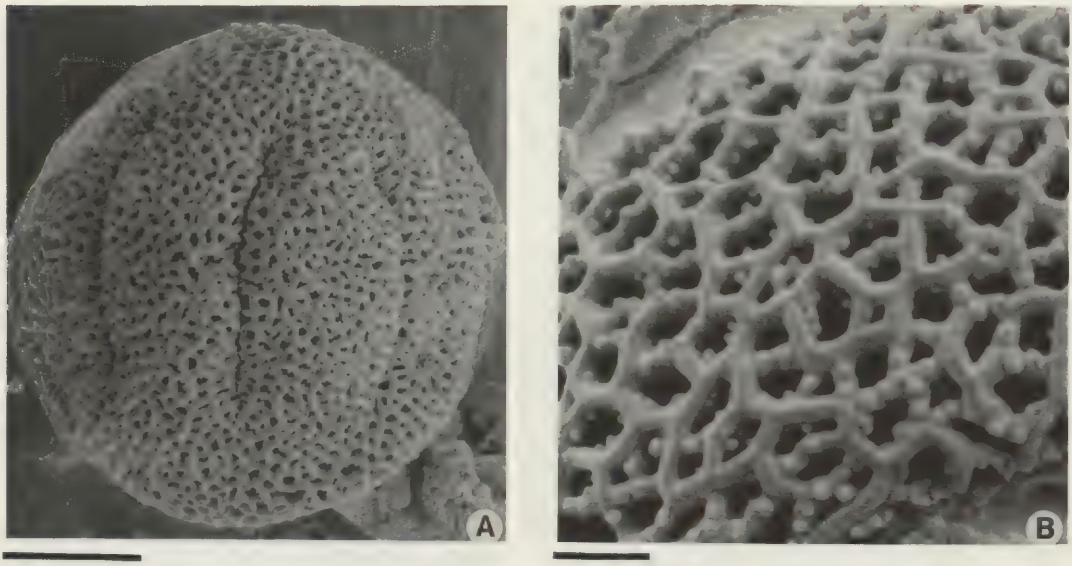

Figura 4. Grano en vista ecuatorial y detalle de la escultura en mesocolpio. —A, B. *Galianthe humilis*, flor longistila (*Hoehne 19357*). Las escalas equivalen a 10 μm en A y 2 μm en B.

Cuadro 2. *Galianthe* subg. *Ebelia*: diferencias respecto al número de aperturas, forma y tamaño de los granos, diámetro de los lúmenes del SR y ancho de los muros del SR y IR. Referencias: obl-esf., oblato-esferoidal; prol-esf., prolato-esferoidal; P, eje polar; E, diámetro ecuatorial; SR, suprarretículo; IR, infrarretículo. Las medidas estan en μm. Respecto al tamaño de los granos se indica las medidas promedio y de los lúmenes del SR, el diámetro mayor.

Especies	Aperturas	Forma	Tamaño P × E	SR muros//lúmenes	IR muros
G. bogotensis					
fl. long.	8–9	obl-esf.	38.6 × 40.8	0.4–0.5//1(2.6)4.5	—
fl. brev.	(7)8–9	obl-esf.	43.0 × 46.5	0.6–0.9//1.4(3.4)4.5	—
G. brasiliensis					
fl. long.	6(7)	prol-esf.	25.7 × 24	0.3–0.4//0.3(1.5)2.9	0.15–0.4
fl. brev.	(6)7	obl-esf./prol-esf.	27.3 × 27.2	0.4–0.7//0.7(2.0)3.3	0.35–0.6
G. brasiliensis subsp. *angulata*					
fl. long.	(8)10	obl-esf.	27.3 × 31.5	—	—
fl. brev.	8–9	prol-esf.	36.8 × 36	0.3–0.6//0.2(1.3)2.8	0.3–0.4
G. cymosa					
fl. brev.	8(9)	prol-esf.	37.6 × 36.7	0.3–0.4//1.4(2.8)5.8	0.3–0.35
G. dichasia					
fl. long	8	subprol.	42.7 × 36.2	0.4–0.5//0.5(1.5)2.0	0.35
fl. brev.	7(8–0)	subprol.	41.5 × 35.3	0.5–0.6//1.0(1.5).18	0.3–0.5
G. dichotoma					
fl. long.	9(10)	obl-esf./prol-esf.	34.0 × 34.2	0.5–0.7//0.8(2.5)3.5	—
fl. brev.	9	obl-esf.	41.5 × 35.3	0.5–0.6//1.0(1.5)1.8	0.3–0.5
G. hispidula					
fl. long.	(7)8	obl-esf.	33.0 × 34	0.3–0.4//0.4(1.2)2	0.2
fl. brev.	(8)9	obl-esf./prol-esf.	34.7 × 34	0.4–0.5//1(1.2)3	0.3–0.4
G. humilis					
fl. long.	8	prol-esf.	37.3 × 36.5	0.4–0.5//1(2.1)3.7	0.3–0.4
G. polygonoides					
fl. long.	(7)8	prol-esf.	28.0 × 26.3	0.3–0.5//0.4(1.4)2.2	0.2–0.35
fl. brev.	(7)8–9	obl-esf.	34.9 × 36.0	0.35//0.9(1.4)3.8	0.35–0.4

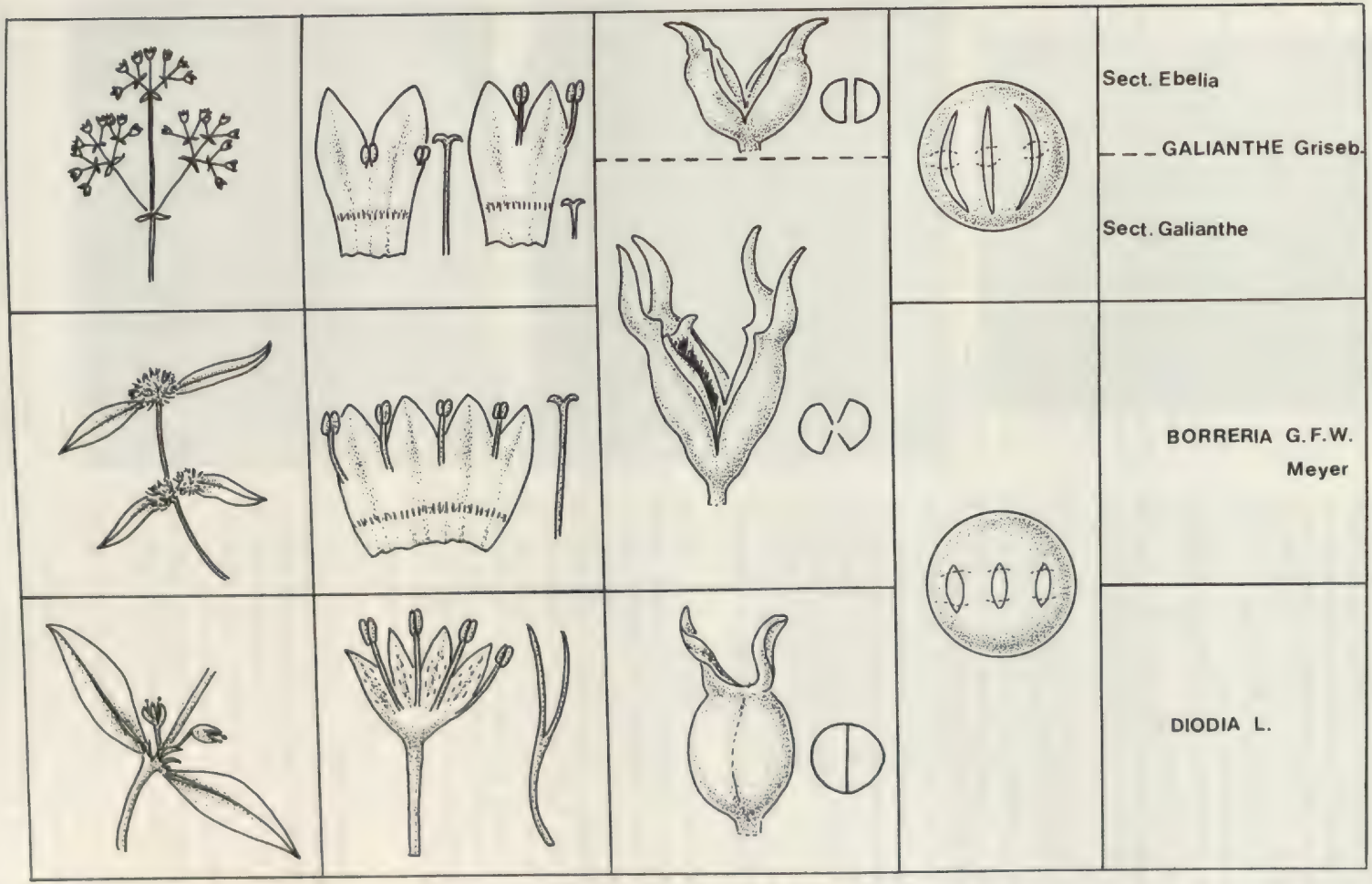

Figura 5. Diferencias y afinidades entre los géneros *Galianthe*, *Borreria* y *Diodia* s. str. sobre la base de sus caracteres exomofológicos (inflorescencia, flor y fruto) y sus caracteres palinológicos. Ver explicación en el texto.

lia y subg. *Galianthe*), *Borreria* y *Diodia* s. str.[3], que se consideran de mayor valor taxonómico:

(1) tipo de inflorescencia: tirsoide, con inflorescencias parciales ± congestas o empobrecidas, cimoides versus glomeriforme o sólo de 1–2–3 flores;
(2) tipo de flor: heterostila (longistila y brevistila) versus homostila;
(3) tipo de fruto: parcial o totalmente dehiscente versus indehiscente;
(4) tipo de polen: semitectado-reticulado, con colpos largos versus tectado-perforado con colpos cortos.

Como se puede apreciar, en las especies del género *Galianthe*, las inflorescencias son terminales y tirsoides y las flores heterostilas. En el subgénero *Galianthe* se agrupan las especies con frutos de mericarpos dehiscentes y en el subgénero *Ebelia* se reúnen las que tienen frutos de mericarpos indehiscentes. En el género *Borreria* las especies presentan frutos como los de *Galianthe* subg. *Galianthe*, pero se separan bien por sus flores homostilas y por sus inflorescencias glomeriformes, terminales y/o axilares. En el género *Diodia* s. str. las flores son isomorfas, axilares, solitarias o en inflorescencias paucifloras y los frutos totalmente indehiscentes.

En cuanto al polen, la estructura de la exina es el carácter más importante para distinguir *Galianthe* de los otros dos géneros; en segundo lugar se encuentra la longitud de los colpos (Fig. 6).

En *Galianthe* se ha estudiado la morfología del polen de más de 30 especies del subgénero *Galianthe* (Pire & Cabral, 1992; Pire, inéd.) en las cuales los granos de polen son semitectados-reticulados, con retículo complejo y zonocolporados, con colpos largos o medianos (ECA/P = 0.40–0.65) (Fig. 6A). En *G.* subg. *Ebelia*, los granos de polen presentan un retículo complejo o, con menor frecuencia, un retículo simple, siendo los colpos predominantemente largos.

En *Borreria* se analizaron cerca de 50 especies (Cabral, 1985; Pire, inéd.[4]) que presentan gran variabilidad en sus caracteres palinológicos; sin embargo la estructura de la exina, tectada-perforada, se mantiene casi constante en todas ellas. En este género los granos de polen pueden ser colporados o porados; cuando son colporados, los colpos son

Figura 6. Granos en vista ecuatorial. —A. *Galianthe centranthoides* (flor brevistila). —B. *Borreria terminalis*. —C. *Diodia virginiana*. Las escalas equivales a 5 µm.

[3] *Diodia* s. str. comprende a las cuatro especies reconocidas por Bacigalupo y Cabral: *D. virginiana* L., *D. kuntzei* K. Schum., *D. macrophylla* K. Schum. y *D. saponariifolia* Cham. & Schldl.

[4] Trabajo presentado en la II International Rubiaceae Conference, Meise, Bélgica (septiembre, 1995).

generalmente cortos (ECA/P = <0.35) (Fig. 6B). Las especies con granos de polen longicolpados poseen exina tectada-foveolada y espínulas localizadas principalmente alrededor de las aberturas.

En cuanto a *Diodia* s. str. (*D. virginiana* L., *D. kuntzei* K. Schum., *D. macrophylla* K. Schum. y *D. saponariifolia* Cham. & Schldl.) posee granos de polen tectado-perforados y con colpos cortos, similares a los ya mencionados para *Borreria* (Fig. 6C).

Con este estudio se demuestra que las especies comprendidas en *Galianthe* subg. *Ebelia* presentan caracteres no sólo exomorfológicos sino también palinológicos que son típicos de *Galianthe*, los que, a su vez, permiten diferenciarlas perfectamente de las de *Borreria* y *Diodia*. Esto apoyaría el criterio de Cabral y Bacigalupo (en este volumen) de ampliar los límites de *Galianthe* creando el nuevo subgénero, *G.* subg. *Ebelia* (Rchb.) E. L. Cabral & Bacigalupo.

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THE TANAKA-KAIYONG LINE—AN IMPORTANT FLORISTIC LINE FOR THE STUDY OF THE FLORA OF EAST ASIA[1]

Li Xi-wen[2] *and Li Jie*[2]

ABSTRACT

The "Tanaka-Kaiyong Line" is a line separating two floristic subkingdoms of East Asia, the Sino-Japanese to the east and the Sino-Himalayan to the west. It lies in the provinces of Sichuan and Yunnan in China. It is comprised of the "Tanaka Line of *Citrus* Distribution" in Yunnan province and the "Kaiyong Line of Orchid Distribution" in Sichuan province, which nearly connect at the border of NW Yunnan and SW Sichuan. After a survey of the distribution patterns of some genera, we are sure that it exists. The Tanaka-Kaiyong Line is significant not only for the subdivision of the East Asia Kingdom and the floristic regionalization of China, but also for the separation of some critical species and the study of vicariance. Moreover, three important floristic regions, the Hengduan Mountain region, Central China region, and Dian–Qian–Gui region, which are noted for species abundance, endemism, and high speciation, are situated near this Line. Compared with Sino-Himalayan genera, the Sino-Japanese are more completely separated by the Tanaka-Kaiyong Line, possibly due to their different florogenetic backgrounds and different times of origin. Additionally, it seems that the centers of biodiversity (or abundance centers) of Chinese endemic genera on each side of the Tanaka-Kaiyong Line are different. The centers on the west side of the Line are mainly neoendemic, but those on the east are mainly paleoendemic. This difference may be caused by geological-geomorphological patterns and the large-scale climatic conditions in China. The formation of Hengduan Mountain and Yunnan Plateau, which was induced by the uplifting of the Himalayas, greatly affected the floristic nature of western East Asia and, therefore, the floristic distributions that led us to define the Tanaka-Kaiyong Line have probably arisen since that time.

Recently in the study on the flora of East Asia it was noted that an important floristic line exists in the western part of East Asia. This line is important in the understanding of the characteristics and biodiversity of the East Asian flora.

I. WHAT IS THE TANAKA-KAIYONG LINE?

The Tanaka-Kaiyong Line is named for the "Tanaka Line" in Yunnan province and the "Kaiyong Line" in Sichuan province. These two lines almost connect at the border of NW Yunnan and SW Sichuan and act as a dividing line between Sino-Japanese and Sino-Himalayan genera.

The Tanaka Line was first suggested by the Japanese scholar Tyôzaburô Tanaka (Tanaka, 1954) in the treatment of the taxonomy and distribution in *Citrus*. Tanaka discovered that a line can be drawn in between the two groups of chains (*Metacitrus* predominating and *Archicitrus* predominating) that is significant in distinguishing the mode of distribution of citrus fruit. This line might be called the "Tanaka Line of *Citrus* Distribution" in connection with the natural development of the *Citrus* flora of the Far East. The approximate position of the Tanaka Line can be shown as a straight line starting at the intersection of 28°N, 98°E southward to approximately 18°45′ or 19°N, 108°E. Tanaka tested the existence of this line by plotting the distribution of the genera in Aurantioideae. Of a total of 22 genera in continental Asia, 10 (45%) do not occur east of the Tanaka Line, while 1 (*Poncirus*) stays inward, totaling 11 genera (50%) that stop at this line. Likewise, a great number of Indo-Malayan plant families stop at this line, as does the westward advance of Sino-Japanese plant families.

The "Kaiyong Line" was first suggested by the Chinese scholar Lang Kaiyong (Lang, 1994) as a line separating the Sino-Himalayan and Sino-Japanese subkingdoms in Sichuan Province. It is based on the distribution patterns of some genera or subgenera of Orchidaceae typical for these two

[1] Dedicated to our advisor, Wu Zheng-yi (Wu Cheng-yih). We congratulate him on his 80th birthday and his great achievements in botanical research, in which he has been engaged for 60 years. We also thank him for his years of tireless teaching. This paper is one of the research reports of the project of "The floristic study on the Chinese seeds plants" (9390010), which was financed by the NSFC. We thank Diana (Nan) Winkelmeyer of the Missouri Botanical Garden for editorial help with the manuscript.

[2] Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650204, People's Republic of China.

subkingdoms because the family is more restricted by environmental conditions than other families. The Sino-Himalayan genera are *Risleya, Diplomeris, Diphylax, Platanthera* subg. *Stigmatosa,* and the Sino-Japanese are *Neofinetia, Vexillabium,* and *Sedirea.* The Kaiyong Line runs north to south as: Naping (Jiuzhaigou), Songpan (Huanglongzhi), Maowen, Guanxian (Guangguanshan), Baoxing, Erlangshan (west of Tianquan), Emei Mountain, Shimian, Xichang, Dechang, Miyi to Panzhihua City. This line is not named by Lang. We named this line the "Kaiyong Line of Orchid Distribution" because Lang was the first person to suggest the line in W Sichuan in the literature and in relation to the Tanaka Line. We have treated the Kaiyong Line as a northern extension of the Tanaka Line because the two are nearly connected, and both act as dividing lines between Sino-Japanese and Sino-Himalayan genera.

II. Significance in Floristic Study

The Tanaka-Kaiyong Line as a dividing line in the flora of East Asia is of great significance in floristic study. It is characterized by the following:

1. It acts as a demarcation for the subdivision of the East Asia kingdom.

Recently many Chinese scholars have suggested East Asia as a floristic Kingdom in the floristic regionalization of the world, because East Asia has no less than 30 endemic families and 577 endemic genera (excluding the Pteridophytes) [according to Wu (1993), but according to Takhtajan (1986), it has more than 20 endemic families and over 300 endemic genera]. In addition, East Asia has a high level of endemic species. The area that comprises Wu's "Sino-Japanese" region is almost the same as the East Asia Kingdom. East Asia borders on the Pacific Ocean with a broad east side and a narrow west side (Fig. 1). It is floristically closely related to the Holarctic Kingdom in the north and the Paleotropic Kingdom in the south. The East Asia Kingdom can be divided into two subkingdoms, the Sino-Japanese in the east and Sino-Himalayan in the west. The floras of these subkingdoms exhibit vicariance between eastern and western taxa, with the line of demarcation situated in western East Asia. The Tanaka-Kaiyong Line evidently divides these two subdivisions on the whole. Because the Line is based on the distribution patterns of the Sino-Japanese genera and the Sino-Himalayan genera, it is of great significance for the subdivision of the East Asia Kingdom floristically, and also for the floristic regionalization of China. Moreover, three important floristic regions are situated near this line: the Hengduan Mountain region on the west and the Central China and Dian–Qian–Gui regions on the east. These three regions have a great abundance of species, the highest levels of endemism at the specific level and speciation in China (Li, 1996).

2. It helps the separation of some critical species and the study of vicariance.

Because the Tanaka-Kaiyong Line divides the Sino-Japanese and Sino-Himalayan floras, it is helpful in the delineation of some critical species belonging to these two floras. The species endemic to one flora are quite different from those endemic to the other, because the floras have different speciation in time and space. For example, *Cyclobalanopsis glauca* (Thunb.) Oerst. of the Sino-Japanese flora is different from *C. glaucoides* Schott. of the Sino-Himalayan flora, although they are very similar morphologically. The concept of the Tanaka-Kaiyong Line helps in separating the species according to their distribution patterns. Vicariance is an important problem in phytogeographical study, and is evident in China between eastern and western taxa, not only for the oaks, conifers, and other evergreen or deciduous trees at low altitudes, but also for hemlocks and firs at high altitudes. For example, *Pinus yunnanensis* Franch. of W China is a vicariant species of *P. massoniana* Lamb. of E China, *Keteleeria evelyniana* Mast. of *K. davidiana* (Bertr.) Beissn., *Castanopsis delavayi* Franch. of *C. sclerophylla* (Lindl.) Schott., *Cyclobalanopsis delavayi* (Franch.) Schott. of *C. gilva* (Bl.) Oerst., *Alnus nepalensis* D. Don of *A. crematogyne* Burkill, and so on. The concept of the Line, together with an analysis of phylogeny, will lead to a determination of what is true and what is false vicariance. It seems that the Line is helpful in the study of the vicariance between the Sino-Himalayan and Sino-Japanese floras.

3. It facilitates understanding of the Sino-Japanese and the Sino-Himalayan elements.

After surveying distribution patterns of some genera in both the Sino-Japanese and the Sino-Himalayan floras (Li & Li, 1992), we are sure that the Tanaka-Kaiyong Line is real. In comparison with the Sino-Himalayan genera, the Sino-Japanese genera follow the line more strictly, perhaps because of their different florogenetic backgrounds and different origin times. In general, the Sino-Himalayan elements are younger and more dynamic, so they do not conform as strictly to the Line,

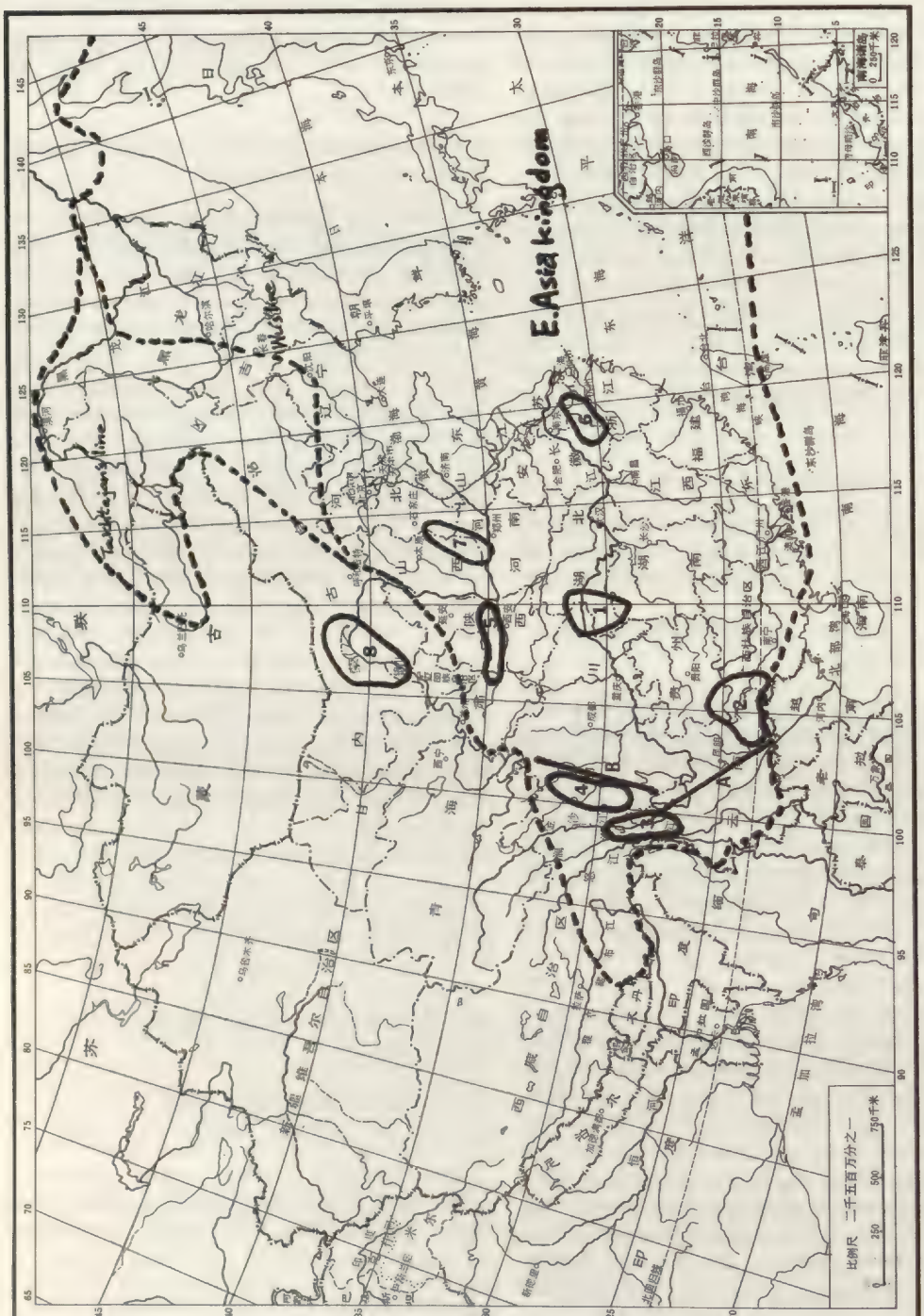

Figure 1. A sketch map of the Tanaka-Kaiyong Line and the centers of biodiversity (or abundance centers) of Chinese spermatophytic endemic genera. Tanaka-Kaiyong Line: A. Tanaka Line; B. Kaiyong Line. Biodiversity centers (or abundance centers) of Chinese spermatophytic endemic genera: 1. Mid-Yangtze center; 2. Dian–Qian–Gui center; 3. South Hengduan Mountain center; 4. Middle Hengduan Mountain center; 5. Qingling center; 6. Huangshan–Tianmushan center; 7. Zhongtiao–South Taihangshan center; 8. South Inner Mongolia center. [Note: Wu's northern border of East Asia is lower than that of Takhtajan (1986).]

and the Sino-Japanese elements are relict, so they conform more strictly to it. This conclusion is in accordance with Wu: "From the florogenetic point of view, the genera of the Sino-Japanese distribution pattern are usually epibiotic and relict in nature, being the historical elements from an ancient Laurasian flora, while the Sino-Himalayan are mixed with several neoendemic elements derived from both Laurasian, Tethyan and Gondwanic elements. The Tethyan origin shows especially in such families as Apiaceae, Boraginaceae, Brassicaceae, Dipsacaceae, Lamiaceae, etc. Probably it implies that the Sino-Japanese distribution pattern is older than the Sino-Himalayan distribution pattern, and also implies that the degree of diversification is stronger and more progressive in Sino-Himalayan flora."

4. IT AIDS THE UNDERSTANDING OF BIODIVERSITY CENTERS (OR ABUNDANCE CENTERS) OF CHINESE ENDEMIC GENERA.

We noted that the centers of biodiversity (or abundance centers) of Chinese endemic genera on each side of the Tanaka-Kaiyong Line are quite different, those west of the Line being mainly neoendemic and those east mainly paleoendemic. According to Ying and Zhang (1984) the west side of the Line has one center of biodiversity, W Sichuan–NW Yunnan, but according to Wang and Zhang (1994) there are two centers, the South Hengduan Mountain center and Middle Hengduan Mountain center. Ying and Zhang's concept of the east side of the Line has two centers, SE Yunnan–W Guangxi and E Sichuan–W Hubei, while Wang and Zhang's concept (Fig. 1) has six: Mid-Yangtze, Dian–Qian–Gui, Qingling, Huangshan–Tianmushan, Zhongtiao–South Taihangshan, and South Inner Mongolia. We think the South Inner Mongolia center, unlike the others, is mainly dry desert, and that Qingling is not a center in a strict sense because it has no endemic genera but supports Chinese endemic genera shared with other regions, especially with Central China (Ying, 1994); thus the east side of the Line has a maximum of four centers in the strict sense for the East Asia Kingdom. Therefore, the different natures of the centers on both sides of the Line are parallel with those of the elements on both sides of the Line. The cause of the difference between the centers of biodiversity on either side of the Line may be directly related to geological-geomorphological patterns and large-scale climatic conditions in China. The area on the west side of the Line is situated on the transitional site from the second to the first terraces geomorphologically and climatically affected by monsoons from both the Indian and Pacific Oceans, while the area on the east side is on the site from the third terrace, or coast land, to the second terrace geomorphologically, and is climatically affected mainly by the monsoons from the Pacific Ocean.

III. Origin of the Floristic Line

The Tanaka-Kaiyong Line, which divides two subkingdoms of the East Asia Kingdom, is a result of the large-scale geological-geomorphological patterns in China, as already mentioned above. Liu and Ding (1984) summarized the history of the geological structure of China. The main Chinese platform had risen above the sea by the end of the Triassic, except that some residual epi-continental waters remained, including one over present-day Yunnan. A trough also extended across what is now the Qinghai–Xizang plateau north of the present Himalayas. From the end of the Jurassic–Cretaceous, a sequence of underthrusts from the south extended the continental land area of China southward and raised the whole platform, particularly in the west. By the end of the Paleocene the present outline of continental China had become established, except that the Himalayan region remained marine until the Eocene. The Himalayas were the product of northward underthrusting of the Indian Plate (Chang & Pan, 1981) and only came into being as a mountain range late in the Cenozoic, or perhaps in the Miocene–Pliocene. It seems that uplift took place at an accelerating rate. The average for the 3000 m rise during the Quaternary is 1.5 mm per year, but the rise during the Holocene may have been four or five times greater (Xu, 1984). The great uplifting of the Himalayas induced the rising and the climatic fluctuation of Henguan Mountain and the Yunnan Plateau, and also greatly affected the floristic nature of the west of East Asia, and the Tanaka-Kaiyong Line thus appeared since that time.

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CHROMOSOME NUMBERS IN COMPOSITAE, XVII: SENECIONEAE III[1]

Harold Robinson[2], *Gerald D. Carr*[3], *Robert M. King*[2], *and A. Michael Powell*[4]

Abstract

A brief review is offered of major chromosome number variations in the Senecioneae based on recent delimitations of the tribe. An additional 78 chromosome reports are provided, including 19 new reports for species, with confirmed or expanded base numbers for the genera *Gynoxys* ($x = 40$), *Lasiocephalus* ($x = 20$), *Pentacalia* ($x = 20$, ca. 50), and *Jessea* ($x =$ ca. 50). The base number for the tribe is $x = 10$, which is found in various multiples. The Blennospermatinae are one of the most distinct groups with a base of $x = 9$, considered an aneuploid reduction from $x = 10$. A new subtribe, Abrotanellinae, is established for the southern South American and southwest Pacific genus *Abrotanella*, which also has $x = 9$ and has often been placed in the Blennospermatinae. Numbers based on $x = 30$ and aneuploid reductions are found in the Tussilagininae, in many Australian *Senecio*, and in the Macaronesian *Pericallis* of the Senecioninae. The origin of such numbers is discussed. An anomalous North American group of *Senecio* (*Packera*) has variable numbers mostly near $n = 23$. Most Western Hemisphere Senecioninae have numbers of $n = 20$ or multiples thereof, with higher numbers in many Andean groups. Numbers of $n = 10$ or lower are mostly restricted to the Eastern Hemisphere, and groups like *Emilia* have recently dispersed from that area. Occurrences of $n = 5$ in *Emilia*, $n = 10$ in some American and Australian *Senecio*, and $n = 14$–16 in some tussilaginoids are considered as reductions.

This paper continues a series dealing with chromosome numbers of Compositae (Raven et al., 1960; Raven & Kyhos, 1961; Ornduff et al., 1963, 1967; Payne et al., 1964; Solbrig et al., 1964, 1969, 1972; Anderson et al., 1974; Powell et al., 1974, 1975; King et al., 1976; Tomb et al., 1978; Robinson et al., 1981, 1985, 1989). This is the third of the series ostensibly dealing with the tribe Senecioneae. It presents an updated summary of the chromosome numbers in the tribe (Appendix 1) and 78 new reports of chromosome numbers, including 19 previously uncounted species listed below in the results (Table 1). The new counts are particularly important in some of the less well known neotropical genera such as the Central American *Jessea* and the Andean *Gynoxys*, *Lasiocephalus*, and *Pentacalia*. Nevertheless, the new counts are not considered to be as important in this paper as the overview of the chromosome number patterns in the tribe, to the extent that they are presently known.

The limits of the Senecioneae in the present paper are in the newer, more restricted sense (Bremer, 1994), following more closely the studies of Nordenstam (1977), Jeffrey et al. (1977), and Jeffrey (1979) and are essentially those of Jeffrey (1992). Previous studies in the present series (Ornduff et al., 1963, 1967), treating the Senecioneae, used the aphyletic traditional concept of the tribe (Bentham & Hooker, 1873) that included, sometimes with reservations, taxa that we now know were misplaced: the cichorioid Liabeae and *Gongrothamnus* (= *Distephanus*, Vernonieae) and the asteroid paleaceous Heliantheae (*Dimeresia*, *Neurolaena*, and *Schistocarpha*), the epaleaceous Heliantheae (*Arnica*, *Mallotopus*, *Peucephyllum*, *Psathyrotes*), and the Inulean *Adenocaulon*. For dispositions of these genera, see the studies of the Liabeae (Robinson, 1983), *Distephanus* (Robinson & Kahn, 1986), and the Heliantheae (Robinson, 1981). Ornduff et al. (1963) also felt that the Blennospermatinae were not Senecioneae, but the subtribe is included in the present concept.

The first paper on the Senecioneae in the present series (Ornduff et al., 1963) had many records and comments on the genera that remain in the tribe. Included were a brief mention of *Crocidium* (of the Blennospermatinae) with $n = 9$, some *Emilia* with $n = 5$, examples of species of *Senecio* in Australia

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[2] Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

[3] Department of Botany, University of Hawaii at Manoa, Honolulu, Hawaii 96822, U.S.A.

[4] Department of Biology, Sul Ross State University, Alpine, Texas 79832, U.S.A.

Table 1. Results. The following are newly reported chromosome counts and citations of vouchers for species of Senecioneae. Species not previously reported are marked with an asterisk (*). K numbers represent King collection numbers. Counts are reported as $2n$ (Carr) or n (Powell). Vouchers are in US (duplicates in MO).

Species	Chromosome number	Voucher
**Arnoglossum ovatum* (Walt.) H. Rob.	$2n$ = ca. 28–30 pairs	U.S.A. Florida: Liberty Co., *K10297*
Barkleyanthus salicifolius (HBK) H. Rob. & Brettell	n = ca. 30	Guatemala. Quezaltenango: *K7261*
B. salicifolius	n = 30	Guatemala. Totonicapán: *K7292*
Crassocephalum crepidioides (Benth.) S. Moore	$2n$ = 20 pairs	Puerto Rico. Mpio. Bayamón, *K10607*
Emilia coccinea (Sims) Sweet	n = 8 or 9	Dominica. St. Patrick, *K6366*
E. fosbergii Nicolson	$2n$ = 10 pairs	Costa Rica. San José: *K10023*
E. fosbergii	n = ca. 10	Ecuador. Guayas: *K6947*
E. fosbergii	$2n$ = 10 pairs	Puerto Rico. Mpio. Salinas, *K10598*
Erechtites hieraciifolia (L.) Raf. ex DC.	$2n$ = 20 pairs	U.S.A. Virginia: Fairfax Co., *K10596*
Erechtites valerianiaefolia (Wolf) DC.	n = 17–20	Dominica. St. George, *K6302*
**Gynoxys acostae* Cuatrec.	$2n$ = ca. 40 pairs	Ecuador. Pichincha: *K10056*
**G. buxifolia* (HBK) Cass.	n = ca. 40	Ecuador. Chimborazo: *K6602*
**G. fuliginosa* (HBK) Cass.	$2n$ = 40 pairs	Ecuador. Carchi: *10117*
**G. hallii* Hieron.	very sticky, possibly n = ca. 40	Ecuador. Pichincha: *K6735*
**G. sancti-antonii* Cuatrec. var. *brevifolia* (Hieron.) Cuatrec.	n = 40 + 4–5 B chromosomes	Ecuador. Azuay: *K6902*
Gynura pseudochina (L.) DC.	n = 10	Thailand. Kamphaeng Phet, *K5438*
**Jessea cooperi* (Greenm.) H. Rob. & Cuatrec.	n = ca. 50	Costa Rica. San José: *K6743*
**J. cooperi*	n = ca. 50	Costa Rica. Cartago: *K6771*
**J. cooperi*	$2n$ = ca. 49 pairs	Costa Rica. San José: *10031*
**Lasiocephalus involucratus* (HBK) Cuatrec.	$2n$ = 20 pairs	Ecuador. Carchi: *K10098*
**L. involucratus*	$2n$ = 20 pairs	Ecuador. Chimborazo: *K10174*
**L. patens* (HBK) Cuatrec.	$2n$ = 20 pairs	Ecuador. Carchi: *K10083*
Pentacalia andicola (Turcz.) Cuatrec.	$2n$ = 20 pairs	Ecuador. Carchi: *K10099*
P. andicola var. *pseudonitidus* Cuatrec.	n = 20	Ecuador. Azuay: *K6643*
**P. firmipes* Greenm.	$2n$ = 20 pairs	Costa Rica. Cartago: *K10022*
**P. phanerandra* (Cufod.) H. Rob. & Cuatrec.	n = 17 or 20	Costa Rica. Cartago: *K6436*
P. reflexa (HBK) Cuatrec.	$2n$ = ca. 50 pairs	Venezuela. Mérida: *K10496*
P. reflexa	$2n$ = ca. 50 pairs	Venezuela. Mérida: *K10590*
**P. sotarensis* (Hieron.) Cuatrec.	$2n$ = ca. 50 pairs	Ecuador. Carchi: *K10078*
P. vaccinioides (HBK) Cuatrec.	n = 20	Ecuador. Azuay: *K6662*
P. vaccinioides	$2n$ = ca. 20 pairs	Ecuador. Carchi: *K10088*
Psacalium sinuatum (Cerv.) H. Rob. & Brettell	$2n$ = ca. 30 pairs	Mexico. Durango: *K9916*
**Pseudogynoxys sonchoides* (HBK) Cuatrec.	n = ca. 46	Ecuador. Azuay: *K6688*
Roldana petasioides (Greenm.) H. Rob. & Brettell	n = 30	Guatemala. Sololá: *K7228*
R. petasioides	n = ca. 30	Guatemala. Quiché: *K7286*
**Senecio canchahuinganquensis* Cabrera	$2n$ = ca. 20 pairs	Argentina. Neuquén: *K9408*
S. costaricensis R. M. King	n = 20	Costa Rica. Cartago: *K5392*, Type
S. costaricensis	n = ca. 17	Costa Rica. San José: *K6759*
S. coahuilensis Greenm.	$2n$ = 23 pairs	Mexico. Coahuila: *K10356*
S. culcitioides Wedd.	$2n$ = 20 pairs	Ecuador. Pichincha: *K10051*
S. deferens Griseb.	$2n$ = 20 pairs	Argentina. Catamarca: *K9465*
S. douglasii DC.	$2n$ = 20 pairs	Mexico. Sonora: *K9806*
S. elegans L.	$2n$ = ca. 10 pairs	Australia. Victoria: *K10268*
S. flavus (Decne.) Sch. Bip.	$2n$ = 10 pairs	Morocco. Quarzazate: *K10653*
S. glomeratus Desf. ex Poir.	$2n$ = 30 pairs	Australia. Victoria: *K9705*
S. gunnii (Hook. f.) Belcher	$2n$ = 20 pairs	Australia. Victoria: *K9767*
S. gunnii	$2n$ = 20 pairs	Australia. Victoria: *K9773*

Table 1. Continued.

Species	Chromosome number	Voucher
**S. hieronymi* Griseb.	$2n = 10$ pairs	Argentina. Buenos Aires: *K10289*
S. jacobaea L.	$2n = 20$ pairs	Australia. Victoria: *K9785*
S. lautus G. Forst. ex Willd.	$2n =$ ca. 20 pairs	Australia. Western Australia: *K9531*
S. lautus	$2n = 10$ pairs	Australia. Western Australia: *K9597*
S. lautus	$2n = 20$ pairs	Australia. Victoria: *K9776*
S. lautus	$2n =$ ca. 20 pairs	New Zealand. North Island: *K10266*
S. linearifolius A. Rich.	$2n = 30$ pairs	Australia. Victoria: *K9739*
S. linearifolius	$2n = 30$ pairs	Australia. Victoria: *K9752*
S. linearifolius	$2n =$ ca. 30 pairs	Australia. Victoria: *K9786*
S. linearifolius	$2n =$ ca. 30 pairs	Australia. New South Wales: *K9975*
S. lucidus (Sw.) DC.	$n =$ ca. 50	Dominica. St. George: *K6379*
S. lucidus	$2n = 50$–52 pairs	France. Martinique: *K10647*
S. madagascariensis Poir.	$2n = 10$ pairs	Australia. New South Wales: *K9972*
S. minimus Poir.	$2n = 30$ pairs	Australia. Victoria: *K9741*
S. nivalis (HBK) Cuatrec.	$2n = 20$ pairs	Ecuador. Pichincha: *K10045*
S. odoratum Hornem.	$2n = 30$ pairs	Australia. Victoria: *K9754*
S. pterophorus DC.	$2n = 10$ pairs	South Africa. Natal: *K10205*
S. pterophorus	$2n = 10$ pairs	South Africa. Cape: *K10215*
S. purpureus L.	$2n = 10$ pairs	South Africa. Cape: *K10212*
S. aff. *purpureus*	$2n = 10$ pairs	South Africa. Natal: *K10207*
**S. rigidus* L.	$2n = 10$ pairs	South Africa. Cape: *K10220*
S. runcinatus Less.	$n = 17$ or 20	Mexico. Veracruz: *K6497*
S. rudbeckiaefolius Meyen & Walp.	$2n = 20$ pairs	Bolivia. Cochabamba: *K9639*
**S. subulatus* G. Don ex Hook & Arn.	$2n = 20$ pairs	Argentina. Río Negro: *K9349*
**S. subumbellatus* Phil.	$2n =$ ca. 20 pairs	Argentina. Mendoza: *K9423*
**S. tephrosioides* Turcz.	$2n = 20$ pairs	Ecuador. Sucumbíos: *K10126*
S. vagans F. Muell.	$2n =$ ca. 49 pairs	Australia. Victoria: *K9750*
S. veilleiodes A. Cunn. ex DC.	$2n =$ ca. 19 pairs	Australia. Victoria: *K9748*
S. veilleiodes	$2n = 19$ pairs	Australia. Victoria: *K9788*
S. viravira Hieron.	$2n = 20$ pairs	Argentina. Río Negro: *K9360*
S. viravira	$2n = 20$ pairs	Argentina. La Rioja: *K9457*
S. warszewiczii A. Br. & Bouché	$n = 20$	Guatemala. Chimaltenango: *K7200*
S. warszewiczii	$n = 20$	Guatemala. Quezaltenango: *K7029*

and the genus *Ligularia* and its relatives with $n = 30$, and a discussion of the *Senecio aureus* group with $n = 22$–24. The paper ends with, "The occurrence of species of *Senecio* with $n = 10$ in portions of Europe and Africa, and the concentration of Senecioninae and Othonninae with $n = 10$ in Africa strongly suggest an Old World origin for the tribe, with subsequent wide migration and diversification nearly throughout the world." These points are enlarged upon below. The present paper adds and discusses a few chromosome records of note from the Andean genera that were previously reported cytologically only by Turner et al. (1967) and Powell and Cuatrecasas (1970).

Within the Senecioneae, at the subtribal and generic levels, two particular microcharacters have come into taxonomic use: (1) the anther collar being cylindrical versus balusterform (with a zone of enlarged cells below, Robinson & Brettell, 1973b; Nordenstam, 1978; Vincent, 1996), and (2) the stigmatic surface covering the whole inside of the style branch versus forming two separated lines on each branch. These characters were observed and illustrated by Cassini (1818), but they were cited only sparingly afterwards until they were used to delimit the generic concepts of *Senecio* sensu lato and the Tussilaginae (as cacalioids) by Robinson and Brettell (1973b) and Nordenstam (1978). This narrower concept of *Senecio* has been resisted by some authors, and the value of the microcharacters has been questioned due to some variability (Wetter, 1983); however, the value of the microcharacters is now generally recognized (Vincent, 1996) and the narrower generic concepts are now generally ac-

cepted (Jeffrey, 1992; Nordenstam, 1996b; Barkley et al., 1996; Vision & Dillon, 1996).

Materials and Methods

The new reports in this paper are based on material collected by R. M. King and counted by G. D. Carr (reported as $2n$) and A. M. Powell (reported as n). The chromosome counts have been made from aceto-carmine or aceto-orcein squashes of microsporocytes in meiosis. Voucher specimens are in US and a second set is at MO.

Discussion

Blennospermatinae, $x = 9$

Ornduff et al. (1963) strongly suggested that *Crocidium* did not belong to the Senecioneae. However, the TEM study of pollen (Skvarla & Turner, 1966) and flavonoid data (Ornduff et al., 1973) support placement of both *Crocidium* and *Blennosperma* in the tribe. Inclusion of *Crocidium* in the Senecioneae, in a subtribe Crocidiinae (= Blennospermatinae), was accepted by Robinson and Brettell (1973a), with the addition of *Ischnea*. The latter addition was supported by the TEM study by Gadek et al. (1989). The subtribe is distinguished within the tribe by small pollen, 23–25 μm diam., measured in fluid, as in the Astereae. Cytologically, *Blennosperma* has $n = 7, 9$; *Crocidium* $n = 9$ (Jeffrey, 1992), and *Ischnea* $n = 9$ (Borgmann, 1964). The subtribe is evidently a basal offshoot of the Senecioneae with an aneuploid reduction series of chromosome numbers from $x = 10$.

Abrotanellinae H. Rob., G. D. Carr, R. M. King & A. M. Powell, subtribus nov., $x = 9$. TYPE: *Abrotanella* Cass.

Plantae herbaceae perennes caespitosae ad 12 cm altae; folia rosulata, laminis glandulo-punctatis; capitula disciformia; flores peripherales feminei, ramis stylorum brevibus, stigmatibus marginalibus; flores interiores masculini vel hermaphroditi; corollae pallidae, tubis interne ad apicem non annulate ornatis, filamenta in partibus superioribus cylindracea; rami stylorum breves vel nulli, stigmatibus marginalibus vel nullis; achaenia glabra vel raro setulifera; grana pollinis 27–40 μm diam.; chromosomatum numerus $2n = 18, 36$.

Abrotanella of South America and the Australasian species that have been placed in that genus were included in the Blennospermatinae by Nordenstam (1977), Bremer (1994), and Swenson (1995a, b), but are excluded from the subtribe here. The base chromosome number of $x = 9$ seems to isolate the group from all members of the Senecioneae except the Blennospermatinae, and *Abrotanella* has glandular-punctate leaves, disciform heads, more incrassate corolla tissue, and no annulus inside at the base of the corolla limb (Robinson & Brettell, 1973a), all of which distinguish it from the Blennospermatinae. The hairs of the achenes, when present, are never the mucilage hairs seen in members of all three genera of the Blennospermatinae. The somewhat larger pollen grains and the texture of the corollas in the Abrotanellinae are more like other Senecioneae than like the Blennospermatinae. The habit of *Abrotanella* is similar to that of *Werneria* and *Xenophyllum*, but the latter clearly belong to the Senecioninae with balusterform anther collars and chromosome numbers of n = ca. 50 or higher in most species.

Tussilaginae, $x = 30$

One group mentioned by Jeffrey (1992) with $n = 30$, the tussilaginoid group or Tussilagininae, contains many mostly Northern Hemisphere genera, some of which were included within *Senecio* in the traditional classification of the tribe (Bentham & Hooker, 1873). The group is characterized by cylindrical anther collars, stigmatic papillae continuous over the inner surface of the style branches, and a strong tendency for palmately veined or peltate leaves. Included are many species outside of Europe that were placed in *Cacalia*, but excluded is *Hasteola* (Anderson, 1994). Sixteen species from various genera with counts of $n = 25, 26, 28, 29$, and 30 were reported by Ornduff et al. (1963, 1967). Counts of $n = 30$ were reported for 15 eradiate, white-flowered Mexican species of the group by Pippen (1968). Counts for a few more Mexican members of the group were reported by Powell et al. (1974). Robinson and Brettell (1974) first generally recognized the Tussilagininae (as the cacalioid group) and correlated it with the chromosome number of $n = 30$, listing the 27 Mexican species then known to have this number. The correlation was also noted by Nordenstam (1977). The Central American genera were reviewed by Barkley et al. (1996) with some recent additions such as *Robinsonecio*, with $n = 30$ (Barkley & Janovec, 1996). The summary of the 35 European, Asiatic, Australian, North American, and Mexican genera of the group by Jeffrey (1992) shows $n = 30$ as the primary or only chromosome number in 25 of the 30 genera that have been sampled cytologically. Some genera have variations from $n = 30$ (Jeffrey, 1992), especially aneuploid reductions: to $n = 25$ or ca. 25 in *Arnoglossum* and *Psacalium*: to $n = 26$ in *Parasenecio, Miricacalia,* and *Syneilesis*: and to n

= 28 in *Rugelia* and *Endocellion*. Lower numbers occur in some genera, within which $n = 30$ predominates: $n = 16$ and 24 in *Ligularia*, $n = 15$ and 20 in *Doronicum*, and $n = 14$ and 16 in *Petasites*.

Although a simple point, it should be noted that $n = 30$ in the Senecioneae is not a simple polyploid derivative of $n = 10$ like $n = 20$, 40, or 80, but requires two steps: first a tetraploid ($n = 20$) crossing with a diploid ($n = 10$) to give a triploid ($2n = 30$), which then is stabilized by a second doubling to $2n = 60$ giving $n = 30$. In the Tussilagininae with lower chromosome numbers, only *Doronicum* has $n = 15$ and 20. *Ligularia* has $n = 16$, with the next lowest number at 24, and *Petasites* has $n = 14$ and 15, with the next lowest number at 26. These lower numbers in the group, of mostly European origin, cannot be ancestral if $n = 30$ is basic to the Tussilagininae. At present, these lower numbers are considered extreme reductions, far exceeding the modest aneuploid reductions seen in other members of the group such as *Arnoglossum*, *Rugelia*, and the Asiatic genera *Parasenecio*, *Miricacalia*, and *Syneilesis*.

While $n = 30$ seems to be basic in the Tussilagininae, that number also occurs in some members of the Senecioninae, mentioned below. Also, the aneuploid reductions in the Tussilagininae approach or duplicate the aneuploid increases in the Senecioninae, e.g., the aureoid group with $n = 22$, 23.

Gynoxoid group, $n = 40$

Jeffrey (1992) listed a few, mostly American, genera as gynoxoid, including *Gynoxys*, *Paragynoxys*, *Paracalia*, and *Aequatorium*. For information on the most recent additions to *Gynoxys*, *Aequatorium*, and *Paragynoxys*, see Robinson and Cuatrecasas (1992). These genera have a single continuous stigmatic surface on the inside of the style branches and cylindrical anther collars like the Tussilagininae, and *Gynoxys* falls generally with the tussilaginoid genera in the cpDNA study of Kadereit and Jeffrey (1996). The one feature that might hold the group apart from the Tussilagininae is the chromosome number of $n = 40$ or ca. 40 in *Paragynoxys* ($n = 38$–40 pairs, Powell & Cuatrecasas, 1970) and *Gynoxys* (Turner et al., 1967; this paper). Counts for two species of *Gynoxys* have been reported previously: *G. hutchisonii* H. Rob. & Cuatrec. (as *G. parvifolia* Cuatrec.) and *G. tomentosissima* Cuatrec. (Turner et al., 1967), with $n =$ ca. 40 or 40 + B's. Counts for five additional Ecuadorian species are reported in the present study, all with $n = 40$ or ca. 40, one of these with 4–5 B chromosomes.

The dioecious genus *Chersodoma* (Dillon & Sagástegui-Alva, 1996) of southern South America has $2n = 20$ (Hunziker et al., 1989) based on one species, *C. argentina* Cabrera, and was placed in the Senecioninae near *Senecio* by Jeffrey (1992). However, the anther collars are cylindrical and the stigmatic surfaces cover the inside of at least the distal halves of the style branches (Robinson & Brettell, 1973b), for which reasons we provisionally place the genus near the Tussilaginae.

Senecioninae

(1) Some elements with $n = 30$ and $n = 50$

The chromosome number $n = 30$ is inevitable in any large group that has a base of $x = 10$ and many multiplies of that number. Of special interest are groups in the Senecioneae that have stabilized at $n = 30$. Jeffrey (1992) mentioned a number of such groups. One in which $n = 30$ seems to be basic is the Tussilagininae. Others appear to be derived separately within the Senecioninae (Jeffrey, 1992), such as *Pericallis* and a group of Australian *Senecio* that was sampled by Ornduff et al. (1963) and studied extensively by Lawrence (1980, 1985a, b).

In the Macaronesian *Pericallis* with 15 species, including the common "Cineraria" of horticulture, $n = 30$ occurs in all eight species that have been counted (Jeffrey, 1992).

A group of Australian species of *Senecio* with $n = 30$ includes one radiate species, five discoid, and four classified as erechtitoid (Lawrence, 1980). Six of the Australian species of *Senecio* with $n = 30$ are self-incompatible perennial herbs, and six others, including *S. biserratus* Belcher, which have $n = 50$, are self-compatible annuals (Lawrence, 1985a, b). Unlike the Tussilagininae with $n = 30$, this group of unusually abundant Australian hexaploids was considered morphologically typical of the genus *Senecio* Lawrence (1985a). Lawrence further suggested that strict autoploidy in the Australian species was unlikely since no known native diploids appeared to exist. However, both diploid and tetraploid counts are reported here for the common Australian species *S. lautus*. As this is the first report of $n = 10$ for an Australian *Senecio*, additional populations of *S. lautus* should be surveyed in order to determine the frequency and extent of this chromosome condition. Regular meiosis without multivalents was observed in the Lawrence study, even in the highest, decaploid, levels.

In the Senecioneae, $n = 50$ has an origin analogous to that of $n = 30$: a cross of $n = 20$ with n

= 30 and a doubling to give $2n = 100$. The number is apparently basic to the Costa Rican/Panamanian species of *Jessea* (Robinson & Cuatrecasas, 1994; Nordenstam, 1996a), included in *Jacmaia* by Jeffrey (1992). Two species were known to have n = ca. 50 (Jeffrey, 1992), and our three counts of *J. cooperi* are the same.

The African *Dendrosenecio* is reported to have chromosome numbers of $n = 10$, ca. 40, and 50 (Jeffrey, 1992); however, Knox and Palmer (1995) and Knox (1996) accepted the conclusions of Knox and Kowal (1993) that the genus consistently has $n = 50$ and the other numbers are in error. Knox and Palmer (1995) stated, "The giant senecios, apparently decaploid ($n = 50$), show virtually no meiotic irregularities that might suggest a recent origin from the predominantly tetraploid ($n = 20$) putatively close relatives suggested in the literature." Knox and Kowal (1993) mentioned many comparatively unrelated elements of the Senecioneae that share the number $n = 50$, including the Australian *Arrhenechthites*, African *Kleinia*, neotropical *Dendrophorbium*, *Graphistylis*, *Jessea* (as *Jacmaia*), *Pentacalia*, and *Xenophyllum* (as *Werneria*). Study of cpDNA indicated that the closest relatives of *Dendrosenecio* are the African genera *Cineraria* ($n = 10$) and *Euryops* (mostly $n = 10$, seldom $n = 20$, 30) (Knox & Palmer, 1995; Knox, 1996). A separate cpDNA study (Kadereit & Jeffrey, 1996) placed *Dendrosenecio* as the most divergent member of a diverse group including the neotropical *Pseudogynoxys* and *Dorobaea* and the Macaronesian *Pericallis*, but unfortunately neither *Cineraria* nor *Euryops* were included in the study.

(2) The aureoid senecios, $n = 22$, 23

The aureoid senecios, often treated as a separate genus, *Packera*, have the appearance and almost all the technical characteristics of *Senecio* sensu stricto. The aureoid species have been treated in *Senecio* as subgroups *Aurei*, *Bolanderiani*, *Lobati*, *Sanguisorboidei*, and *Tomentosi* in Ornduff et al. (1963, 1967), with reports of $n = 22$, 23, or 24 from 22 species. Additional records were provided by Kowal (1975) and Bain (1985), and the group was discussed by Barkley (1988), who stated that chromosome numbers had been reported for 48 of the 59 species. Our count of $n = 23$ for the Mexican *Senecio coahuilensis* agrees with previous reports for the species and is the commonest number in the group. Some 15 or 16 species occur in Mexico (Freeman & Barkley, 1995; Barkley et al., 1996). Counts of $n = 20$ for *Senecio flettii* Wiegand and *S. bellidifolius* HBK are anomalous in the aureoid group (Barkley, 1988), but *S. bellidifolius* is well nested within the aureoid group on the basis of ITS sequence data and pollen structure (Bain & Jansen, 1995). Kowal (1994) cited ca. 65 species in the group, all in North America from Mexico to the Arctic, with one Arctic-alpine species extending into Asia. Most species have $n = 23$, and $n = 22$ occurred only in seven species in the area of most diversity, including four species restricted to eastern North America (Kowal, 1994). Counts of $n = 20$ and 40 in *Senecio pseudaureus* were probably wrong (Kowal, 1994).

Packera, with *Senecio aureus* L. as type, was accepted as a genus by Jeffrey (1992) using such structural characters as lack of interfascicular cambium, branching fibrous roots, apparently obscure carpopodia, and specific forms of apically flagellate hairs, which are neither exclusive to the aureoid group nor very convincing. The group lacks the fluked pappus of typical *Senecio* (Drury & Watson, 1966), but so do many other elements of *Senecio*. A more substantial difference is the helianthoid ultrastructure of the pollen wall (exine with internal foramina), which occurred in all 19 aureoid species examined in sections *Aurei*, *Tomentosi*, and *Lobati* (Bain & Walker, 1995), and the latter authors questioned the value of continuing to recognize the sections. Non-aureoid North American species examined, including some tephroseroid Senecioneae (*Tephroseris*, Tussilagininae, $x = 24$) and the *Senecio* sections *Lugentes*, *Integerrimi* ($n = 20$), and *Triangulares* ($n = 10$, 18, 20, 40), had a senecioid exine wall pattern (lacking internal foramina).

A few features of the aureoid senecios are clear. It is the only significant element of the Senecioneae in which the chromosome number does not readily fit the general pattern derived from $x = 10$ and its multiples, although it may have been derived by an aneuploid increase from groups with $n = 20$, to which it seems otherwise closely related. The number $n = 20$ has been reported in the group (Barkley, 1988), but Kowal (1994) considered this an error. Also, the number n = ca. 30 has been reported for *S. sanguisorbae* DC. (Turner et al., 1961), for which all other counts are $n = 23$. Chromosome numbers of this group might be more unstable than in taxa with $x = 10$, 20, 30, or 50.

Unfortunately, the best characters differentiating the aureoid senecios have limited value for ordinary taxonomic identification. Neither chromosome number nor ultrastructure of the pollen exine is readily observable. The lineage is distinct, but the phyletic distance from typical *Senecio* may still be comparatively slight. *Senecio aureus* falls into a group of intermixed *Senecio–Kleinia–Gynura* species in the cpDNA study of Knox and Palmer (1995). The evidence could be used to justify many further seg-

regates from *Senecio*, but the necessary detailed studies are still to be done. Recognition of *Packera* as a distinct genus seems premature at this time.

(3) *Mulgedifolii* group, $n = 20, 40$

The *Mulgedifolii* group of Mexico lacks ray florets and has red or white, but never yellow, corollas. The combination of characters led some early authors to place some of the species in the broad concept of *Cacalia*, and they appear among the excluded taxa listed by Pippen (1968). The *Mulgedifolii* have the characteristic balusterform anther collars and separate stigmatic lines of the Senecioninae. The group was retained in *Senecio* by Barkley et al. (1996). There is a report of $n = 22$ for *S. runcinatus* Less. (Keil & Stuessy, 1975), and the same species is reported here as $n = 17$ or 20. Kowal (pers. comm.) has indicated that the $n = 22$ was probably wrong. The unpublished summaries of the *Mulgedifolii* chromosome counts by Villaseñor list 10 counts for 6 species (1986) and 33 counts for 15 of the 17 species (1991). All listed counts, except the dubious $n = 22$, are $n = 20$ with one tetraploid $n = 40$.

(4) *Emilia*, $n = 5$

Emilia continues to show chromosome numbers of $n = 5$ and 10 (Baldwin, 1946). The related African species of *Senecio* that were reported with $n = 5$ by Turner and Lewis (1965) and Lawrence (1985a, b) have all been transferred to *Emilia* by Jeffrey (1986). The lower numbers correlate with the short-lived, weedy habit of the genus. This situation parallels that of *Fleischmannia microstemon* (Cass.) K. M. King & H. Rob. (Baker, 1967) and many other short-lived species with lower DNA content (Bennett, 1972). The low number is considered here a derived condition in *Emilia*, a reorganization of chromatin on fewer centromeres as in *Fleischmannia microstemon* (Baker, 1967) and *Crepis* (Tobgy, 1943). Such a reorganization, or "genome congealing" (Wagner et al., 1993: 422–423) has been supported by a measurement of the nuclear DNA content of *E. discifolia* (Oliv.) C. Jeffrey (as *Senecio discifolius* Oliv.) (Lawrence, 1985b).

In structural features, *Emilia* is a member of the Senecioninae, with paired stigmatic lines and balusterform anther collars, and comes out in the general subgroup with *Othonna* and *Dendrosenecio* in the cpDNA study of Kadereit and Jeffrey (1996).

(5) Senecioninae with $n = 10, 20$

In the Senecioneae, $n = 10$ is largely restricted to Europe and Africa in the Eastern Hemisphere (Ornduff et al., 1963), and the pattern is reinforced by new reports in the present study. A few interesting exceptions occur. *Emilia*, with $n = 5$ and 10, is only a recent introduction into the New World from the Old World. The one old citation of $n = 10$ in the neotropical *Pseudogynoxys*, questioned by Jeffrey (1992), must be incorrect. All other reports for the genus are $n = 45–48$ including *P. chenopodioides* (HBK) Cabrera with $n = 45 + 5$ (Turner et al., 1962, as *S. confusus* Britton) and our report of *P. sonchoides* (HBK) Cuatrec., representing two morphological extremes of the genus. Jeffrey's (1992) summary also gives both $n = 10$ and $n = 20$ for *S. flaccidus* Less. of Mexico and *S. brasiliensis* (Spreng.) Less. of South America. These isolated occurrences of $n = 10$ in basically $n = 20$ groups seem unlikely to be survivors of an ancestral number, but are more likely reductions resulting from polyhaploidy or aneuploid reduction as in *Emilia* and some Tussilagininae such as *Doronicum*, *Ligularia*, and *Petasites*.

An interesting close relationship between an African species with $n = 10$ and an American species with $n = 20$, both autogamous, annual, desert species, is suggested by isozyme analysis (Liston et al., 1989) and cpDNA evidence (Liston & Kadereit, 1995). In these papers, the North American *Senecio mohavensis* A. Gray was considered a closely related derivative, through long-distance dispersal, of *S. flavus* (Decne.) Sch. Bip. subsp. *breviflorus* Kadereit of the Saharo-Arabian deserts.

Radford et al. (1995) indicated that the aggressively weedy taxon commonly identified as *Senecio madagascariensis* Poir. was consistently $2n = 20$ based on material from Madagascar, South Africa, Australia, and Argentina specimens, and our count is the same. In contrast, Radford et al. (1995) reported the common Australian species *S. lautus* G. Forst. ex Willd. as consistently $2n = 40$ (see also the present study; Turner, 1970; Lawrence, 1980; Webb, 1988). However, see the report here of $2n = 10$ pairs for material determined by Lander, Short, and Wilson as *S. lautus* from Western Australia. Sindel (1996) summarized the literature on the four subspecies of *S. lautus*.

(6) Andean genera *Lasiocephalus* and *Pentacalia*, $n = 20, 30, 45–52$

Our counts confirm the few previous counts for two Andean genera. Further work on chromosome numbers of Andean Senecioneae is needed. *Lasiocephalus* (including *Aetheolaena*) has previously been known cytologically from one species, *L. loeseneri* (Hieron.) Cuatrec. (Turner et al., 1967). Counts for additional species, *L. involucratus* (HBK) Cuatrec. and *L. patens* (HBK) Cuatrec., are reported in the present study. All three species show $n = 20$.

Robinson and Cuatrecasas (1978) resurrected *Pentacalia* from synonymy within *Senecio* and in-

cluded 13 Central American species. Cuatrecasas (1981) transferred 177 South American species into *Pentacalia*. He accepted two subgenera, the often scandent subgenus *Pentacalia* and the often heath-like subgenus *Microchaete*. Jeffrey (1992) split *Pentacalia* into three groups: typical *Pentacalia*; a new genus *Monticalia* Jeffrey, roughly equivalent to the subgenus *Microchaete*; and a broadly delimited genus *Dendrophorbium*. The broader view of *Pentacalia* is retained here because of some unresolved problems of intergradation. In personal discussion, Cuatrecasas pointed out that, while most members of subgenus *Pentacalia* are scandent, the type species, *P. arborea* (HBK) H. Rob. & Cuatrec., and its closest relatives are trees with hanging branches. The isolated branches can be mistaken for vines. Thus, the nature of the type species complicates any tendency to base generic distinctions on habit. The genus *Monticalia* is not considered distinct from *Pentacalia* here. In any case, priority would go to *Scrobicaria*, which was imperfectly distinguished from *Monticalia* only by its opposite leaves and which was recently reduced to synonymy under *Pentacalia* (Cuatrecasas, 1994). *Dendrophorbium* is also interpreted more narrowly here to include only its more typical element that usually lacks tails on the bases of the anthers. As a result, the following chromosome counts cited by Jeffrey (1992) all fall within *Pentacalia* sensu lato: *Pentacalia* $n = 20$ (1 sp.), ca. 40 (1 sp.), 45–50 (2 spp.), 50 (1 sp.), and ca. 51 (1 sp.); *Dendrophorbium* $n =$ ca. 40, 49–50 based on 1 sp.; and *Monticalia* $n = 20$ (9 spp,) and 40 + 1–5 (1 sp.). The reports in the present study, of which three are new, show the same range of numbers, $n = 20$, $n = 17$ or 20, and $n =$ ca. 50. The higher numbers in *Pentacalia* have undoubtedly arisen many separate times in higher elevation members of the genus.

Senecio lucidus (Sw.) DC., from the Lesser Antilles, is reported here with $n =$ ca. 50 and $2n =$ 50–52 pairs. The species evidently belongs to *Pentacalia*, but dispositions of West Indian species of the group are very incomplete (Robinson, 1982).

(7) *Culcitium* and *Dorobaea*, $n = 20, 50$

Culcitium sensu stricto ($n = 20$) and *Dorobaea* ($n =$ ca. 50), from the northern Andes, have fistulose receptacles and a rosulate habit with decrescent or progressively smaller upper leaves. For these reasons, Jeffrey (1992) and others, including Robinson, have considered both genera as part of *Senecio*, in spite of their individually distinctive appearances. Recent cpDNA evidence placed *Dorobaea* in a lineage with *Dendrosenecio* and *Pseudogynoxys*, less close to *Emilia* and *Othonna*, and isolated from *Senecio* sensu stricto (Kadereit & Jeffrey, 1996). Both Andean genera have stigmatic lines and anther collars of the Senecioninae. On the basis of the cpDNA study, *Dorobaea* (3 sp., Nordenstam & Pruski, 1995) and the probably closely related *Culcitium* sensu stricto are recognized here as distinct genera.

(8) *Werneria* and segregates, $n =$ ca. 50, 100

Werneria has been treated very broadly in the past to include many densely leaved, rosulate or strobiform species in tropical America specialized for high elevations. Genera recently segregated by Funk (1997a, b, c) are *Xenophyllum*, including two species with $2n =$ ca. 104 ± 4 and $2n =$ ca. 108 ± 4 (Diers, 1961), and the monospecific *Misbrookea*, with $n =$ ca. 106 ± 4 (Diers, 1961). The type of *Werneria*, *W. nubigena* HBK, has been reported as $2n =$ ca. 212 ± 8 from Peru (Diers, 1961) and as $n = 50$ from Guatemala (Beaman & Turner, 1962). Other Andean species that presently remain in *Werneria*, for which Diers's (1961) counts are available, include *W. apiculata* Sch. Bip. with $2n =$ ca. 206 ± 8, *W. orbignyana* Wedd. with $2n =$ ca. 100 ± 4, *W. caespitosa* Wedd. with $2n =$ ca. 154 ± 6, *W. pygmaea* Gillies ex Hook. & Arn. with $2n =$ ca. 212 ± 8, *W. solivifolia* Sch. Bip. with $2n =$ ca. 42 ± 2, *W. spathulata* Wedd. with $2n =$ ca. 106 ± 4, and *W. villosa* A. Gray with $2n =$ ca. 150 ± 6. The high chromosome numbers that predominate in the group are evidently associated with the harsh environment of the high-elevation Andes.

Adenostylinae Benth. & Hook. f., $x = 20$

Jeffrey (1992) recognized, within his Senecioninae, a Eurasian group of perennial rhizomatous herbs with 4-lobed corollas. The group includes the genus *Cacalia* ($n = 19$), in its Linnaean sense (Robinson & Brettell, 1973b), which is the same as the later-named *Adenostyles*, and the subtribal name Adenostylinae is applied here. Other genera included in the group are *Dolichorrhiza* ($n = 15$–16, 20, 22), *Iranecio* ($n = 12$, 20), and *Pojarkovia* ($n = 20$) (Jeffrey, 1992). A fifth genus, *Caucasalia* ($n = 19$), has been described by Nordenstam (1997), who has suggested base numbers of $n = 20$ for *Dolichorrhiza*, *Iranecio*, and *Pojarkovia*. The distribution of the numbers suggests more than one aneuploid reduction series from $x = 20$.

Conclusions

Comparisons between recent taxonomy in the Senecioneae and available chromosome counts have demonstrated again the important point already suggested in the study of the Heliantheae (Robinson et al., 1981): that a phyletic taxonomy can rare-

ly be constructed primarily on the basis of chromosome counts, but chromosome counts usually make sense at some level when compared with a phyletic taxonomy. The positions of the most divergent elements of the tribe, Blennospermatinae and Abrotanellinae, with $x = 9$, could have been foreseen using either taxonomic or cytological approaches. In the remainder of the Senecioneae, significant chromosome number patterns usually recur frequently, such as $x = 30$ in the distinctive Tussilaginae but also in a number of separate elements of the Senecioninae. Some of the more unique chromosome number trends in the tribe, such as $n = 5$ in *Emilia* and $n = 22, 23$ in the aureoid group of *Senecio*, are taxonomically comparatively close to typical *Senecio*. Some genera such as *Dendrosenecio* of Africa, the Macaronesian *Pericallis*, the tropical American *Jessia* and *Pentacalia*, and an Australian group still placed in *Senecio*, seem to stabilize at counts of $n = 30$ and $n = 50$. Still other members of the tribe, including some related pairs of species in *Senecio*, show simple polyploid variations between $n = 10$ and $n = 20$.

Some taxonomically distinctive groups of the Senecioneae show distinctive chromosome counts. Nevertheless, separate elements of the tribe with the same counts and evidence of different numbers in closely related groups indicate the peril of trying to justify generic or subtribal distinctions in the tribe solely on the basis of chromosome counts.

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Appendix 1. General distributions, habit, and apparent basic chromosome numbers, geographical ranges, and habits of genera of the Senecioneae. Arrangement follows the genera and some of the groupings of Jeffrey (1992) with numerous modifications to coincide with discussions in the text.

Genus	General distribution	Habit	Chromosome number
Blennospermatinae			
Blennosperma Less.	W U.S., Chile,	annual herbs	$n = 7, 9$
Crocidium Hook.	W U.S.	annual herbs	$n = 9$
Ischnea F. Muell.	New Guinea	annual herbs	$n = 9$
Abrotanellinae			
Abrotanella (Gaudich.) Cass.	S South America, SW Pacific	perennial herbs	$n = 9, 18$
New Guinea Montane Endemic Group			
Papuacalia Veldkamp	New Guinea	woody	$n = 36$
Tussilagininae			
Traversia Hook. f.	New Zealand	shrubs	$n = 30$
Bedfordia DC.	Australia	small trees	$n = 30$
Brachyglottis J. R. Forst. & G. Forst.	New Zealand & Tasmania	shrubs	$n = 30$
Telanthophora H. Rob. & Brettell	Mexico, Central America	weak shrubs	$n = 30$
Pittocaulon H. Rob. & Brettell	Mexico, Central America	seasonally deciduous shrubs	$n = 30$
Barkleyanthus H. Rob. & Brettell	U.S., Mexico	shrubs	$n = 30$
Roldana La Llave	SW U.S., Mexico, Central America	subshrubs, shrubs	$n = 30$
Digitacalia Pippen	Mexico, Guatemala	perennial herbs	$n = 30$
Psacalium Cass.	U.S., Mexico	rosulate perennial herbs	$n =$ ca. 25, ca. 29, 30
Pippenalia McVaugh	Mexico	rosulate perennial herbs	$n = 30$
Robinsonecio T. M. Barkley & Janovec	Mexico, Guatemala	perennial herbs	$n = 30$
Luina Benth.	Mexico	subshrubs	$n = 30$
Cacaliopsis A. Gray	W U.S.	perennial herbs	$n = 30$
Rugelia Shuttlew. ex Chapm.	E U.S.	perennial herbs	$n = 28$
Arnoglossum Raf.	E U.S.	perennial herbs	$n = 25, 26, 27, 55$
Tetradymia DC.	W U.S., Mexico	shrubs	$n = 30$
Lepidospartum A. Gray	W U.S., Mexico	shrubs	$n = 30$, ca. 45
Dolichoglottis B. Nord.	New Zealand	perennial herbs	$n = 30$
Dendrocacalia (Nakai) Nakai ex Tuyama	Bonin Island	weak shrubs	$n = 30$
Farfugium Lindl.	E Asia	perennial herbs	$n = 30$
Ligularia Cass.	Europe, Asia	perennial herbs	$n = 24, 27, 29, 30$
Cremanthodium Benth.	Asia	perennial herbs	$n = 29$
Sinacalia H. Rob. & Brettell	China	perennial herbs	$n = 30$
Parasenecio W. W. Sm. & Small	E Asia, Aleutians	perennial herbs	$n = 26, 29, 30, 60$
Miricacalia Kitam.	Japan	perennial herbs	$n = 26, 27$
Syneilesis Maxim.	E Asia	perennial herbs	$n = 26, 39$
Doronicum L.	Europe	perennial herbs	$n = 15, 20, 30, 60$
Homogyne Cass.	Eurasia	perennial herbs	$n = 30, 60, 70, 80$
Tussilago L.	Eurasia	perennial herbs	$n = 30$
Endocellion Turcz.	N & E Asia	perennial herbs	$n = 28, 29, 30$
Petasites Mill.	Eurasia, North America	perennial herbs	$n = 14, 16, 26, 28, 30$
Sinosenecio B. Nord.	S & SE Asia, W North America	perennial herbs	$n = 23, 24$
Nemosenecio (Kitam.) B. Nord.	E Asia	perennial herbs	$n = 24$
Tephroseris (Rchb.) Rchb.	Central Europe, Arctic	perennial herbs	$n = 24, 25$

Appendix 1. Continued.

Genus	General distribution	Habit	Chromosome number
Gynoxoid			
Paragynoxys (Cuatrec.) Cuatrec.	N Andes	shrubs, trees	n = ca. 40
Gynoxys Cass.	N Andes	shrubs	n = 40, ca. 40
Chersodoma			
Chersodoma Phil.	S South America	perennial herbs, subshrubs	n = 10
Senecioninae, numbered groups discussed in text.			
(1) Some generic groups with n = 30 or 50, some with penicillate styles.			
Jessea H. Rob. & Cuatr.	Central America	perennial herbs	n = ca. 50
Robinsonia DC.	Juan Fernandez	weak shrubs	n = 20
Lordhowea B. Nord.	SW Pacific	shrubs	n = 19
Arrhenechthites Mattf.	New Guinea	shrubs	n = ca. 50
Dendrosenecio (Hauman ex Hedb.) B. Nord.	Central Africa	rosette-trees	n = 50
Pericallis D. Don	Macaronesia	perennial herbs	n = 30
Graphistylis B. Nord.	Brazil	perennial herbs	n = 50
Iocenes B. Nord.	Argentina, Chile	perennial herbs	n = 20
Cineraria L.	E & S Africa, Arabia	herbs	n = 10
(2, 3) *Senecio* including aureoid group and *Mulgedifolii.*			
Senecio L. (incl. *Packera* A. Löve & D. Löve)	America, Eurasia, Africa, Australia	annual & perennial herbs	n = 10, 18, 19, 20, 22, 23, 30, 40, 46, 50, etc.
(4) *Emilia,* n = 5.			
Emilia (Cass.) Cass.	paleotropics, wide adventive	annual herbs	n = 5, 8, 10, 15
(5) Genus discussed with *Senecio* under Senecioninae with n = 10, 20.			
Pseudogynoxys (Greenm.) Cabrera	tropical America	vines	n = 45, ca. 46
(6) Andean genera *Lasiocephalus* and *Pentacalia,* n = 20, 30, 45–52.			
Lasiocephalus Schltdl.	N Andes	spreading subshrubs	n = 20
Pentacalia Cass. (incl. *Scorbicaria* Cass. & *Monticalia* C. Jeffrey)	Central America, West Indies, South America	shrubs & vines	n = 20, ca. 40, 45–50, 50
Odontocline B. Nord.	West Indies	scandent shrubs	n = 30
(7) *Culcitium* and *Dorobaea,* n = 20, 50.			
Culcitium Humb. & Bonpl.	Andes	perennial herbs	n = 20
Dorobaea Cass.	Andes	perennial herbs	n = ca. 50
(8) *Werneria* and segregates, n = ca. 50, 100.			
Werneria HBK	Andes	perennial herbs	n = ca. 48, 50, 52, ca. 75, ca. 77, ca. 103, ca. 106
Misbrookea V. A. Funk	Andes	perennial herbs	n = ca. 53
Xenophyllum V. A. Funk	Andes	perennial herbs	n = ca. 50, 54
Other Senecioninae not discussed in text, giving Jeffrey (1992) subgroups.			
(Senecionoid)			
Hasteola Raf. (incl. *Synosma* Raf. ex Britton & A. Br.)	E U.S.	perennial herbs	n = 18, 20
Erechtites Raf.	North & South America	perennial herbs	n = 20
Crassocephalum Moench	tropical Africa, Asia, adventitious	perennial herbs	n = 10, 20

Appendix 1. Continued.

Genus	General distribution	Habit	Chromosome number
(Synotoid)			
Faujasiopsis C. Jeffrey	Mauritius	shrubs	$n = 10$
Synotis (C.B.Cl.) C. Jeffrey & Y. L. Chen	E Asia	subshrubs	$n = 10, 18, 20$
Delairea Lem.	South Africa	scandent	$n = 10$
(Gynuroid)			
Solanecio (Sch. Bip.) Walp.	tropical Africa	herbs, weak shrubs	$n =$ ca. 90
Kleinia Mill.	Macaronesia, Africa, S Asia	fleshy herbs, shrubs	$n = 9, 10$
Gynura Cass.	paleotropics	scandent herbs	$n = 10$
(Othonnoid)			
Steirodiscus Less.	South Africa	annual herbs	$n = 8, 10$
Othonna L.	South Africa, SW Asia, Australia	succulent perennial herbs, subshrubs	$n = 10, 20$
Gymnodiscus Less.	South Africa	annual herbs	$n = 9$
Euryops (Cass.) Cass.	tropical & South Africa, Arabia	annual & perennial herbs, subshrubs	$n = 10, 20$
Adenostylinae (quadridentate group)			
Iranecio B. Nord.	SW Asia	rhizomatous herbs	$n = 12, 20$
Dolichorrhiza (Pojack.) Galushko	Caucasus, Iran	rhizomatous herbs	$n = 15–16, 20, 22$
Pojarkovia Askerova	Caucasus	rhizomatous herbs	$n = 20$
Cacalia L.	Europe	rhizomatous herbs	$n = 19$
Caucasalia B. Nord.	Caucasus	rhizomatous herbs	$n = 19$

BOOK REVIEW

Mori, S. A., G. Cremers, C. Gracie, J.-J. de Granville, M. Hoff & J. D. Mitchell. 1997. Guide to the Vascular Plants of Central French Guiana. Part 1. Pteridophytes, Gymnosperms, and Monocotyledons. Hardcover. ISBN 0-89327-398-8. Memoirs of the New York Botanical Garden 76(1): 1–422. Retail price: $50 U.S.

In a time when many country-wide or regional floras are under way in tropical America, yet few are close to completion, it is refreshing to see that a new round of smaller neotropical floras is being completed. The *Guide to the Vascular Plants of Central French Guiana* follows the recently published *Flora of St. John* by Pedro Acevedo and will soon be succeeded by a florula of several biological reserves around Iquitos, Peru, by Rodolfo Vásquez and a florula of Amacayacu National Park in Amazonian Colombia by Agustín Rudas. Within the next year or two we should also be regaled by an illustrated field guide and a separate flora of the Reserva Ducke outside Manaus, Brazil. Each of these floras covers between 1000 and 3000 taxa and will provide a solid baseline of plant data that will facilitate more in-depth studies at these sites in the future.

This first of two volumes of the Central French Guiana flora covers the pteridophytes (194 spp.), gymnosperms (1 sp.), and monocotyledons (426 spp.), as well as a brief introduction, an extensive "Aids to Identification" section, a key to the major groups of plants, and a glossary of botanical terms at the end. Informative and easy-to-use keys are also provided for the families of monocotyledons and pteridophytes. Volume 2, which is due out in late 1998, will cover the estimated 1435 species of dicotyledons in the study area, for a total of just over 2150 species of vascular plants in the whole flora. The area covered by this flora is 1400 km^2, although the level of knowledge and collecting is clearly concentrated on the immediate surroundings of the village of Saül. I was at first confused when looking at the map of the flora area (fig. 2), because the scale indicates a much larger area. To correlate with the given coordinates and the stated size of the flora area, the scale bar should read "7 km" instead of "20 km."

The beauty of this book is that it is so lavishly illustrated. There are 240 excellent color photographs by Carol Gracie of plant species and their distinguishing characters, interspersed in small fascicles throughout the text. There are also 165 line drawings, most of them illustrating individual species, but 8 of these (figs. 4–11) are exquisite full-page composite drawings by Bobbi Angell that show features such as different fruit types, leaf glands, and adaptations for climbing. Two more full-page figures in the glossary pack in a multitude of useful characters as well.

I have just a few quibbles with the style and layout of the volume. The size of the type is too small, at least where there are pages of uninterrupted text. I would like to see more precise or informative headers used, for example, family names rather than the few high level groups used on recto pages or the same journal name repeated throughout on the verso pages. The "Aids to Identification" section provides a myriad of valuable field characters, but the lists go on for a full 36 pages, and a single list such as "Trees, shrubs, and lianas with glands on the leaves" covers 2½ pages with 57 bulleted entries. There are clearly three very different styles of illustrations combined in the volume. Bobbi Angell's drawings of the monocots (except palms) are typically elegant and delicate. The palms, however, are excessively dark and too highly contrasted. Last, the pteridophyte figures use dashed lines to separate different species on the same page and then label them with overly bold-faced, Leroy-drawn species names. The photographic inserts are treated as "plates" to distinguish them from the black-and-white "figures," but then they are numbered with Roman numerals, which presents a minor challenge when the text refers the reader to "Plate LXXII." Toward the end of the volume there is a nine-page "Index to species illustrated in Part 1," but since the general index already does a fine job of referencing all the figures and plates, I would recommend not repeating this kind of index in the next volume.

The taxonomic treatments were prepared mostly by specialists in the particular families, and the careful degree of editing is apparent throughout. Specialized families such as the orchids, grasses, and sedges have separate figures that effectively illustrate the main descriptive characters used in the treatments. The scope of the descriptions, whether family, genus, or species, is not universal but rather is restricted to the flora area itself. Consequently, the claim that the flora will help identify families and genera from other lowland areas in northern South America will not always hold up.

Still, botanists from as far away as Manaus have found a great deal of overlap with this area and their own local flora. One helpful addition would be to include some information about each species' overall distribution, for instance, if it is a narrow endemic or a widespread American weed.

Altogether, this volume ranks right at the top of its class. It follows the tradition of extremely informative local floras like Tom Croat's *Flora of Barro Colorado Island* and then provides the kind of visual aids that will entice even casual aficionados to explore the flora of lowland South America, be it vicariously, browsing through this book, or by getting their feet dirty and visiting a now well-documented site such as the region surrounding the French Guiana village of Saül.—Paul E. Berry, *Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A.*

NOTICE

The 1997 Jesse M. Greenman Award

The 1997 Jesse M. Greenman Award has been won by Elena Conti for the publication "Circumscription of Myrtales and their relationships to other rosids: Evidence from *rbc*L sequence data," co-authored by E. Conti, A. Litt, and K. J. Sytsma, and published in American Journal of Botany 83(2): 221–233 (1996). This study is based on a Ph.D. dissertation from the University of Wisconsin under the direction of Dr. Kenneth J. Sytsma.

The Greenman Award, a certificate and a cash prize of $1000, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1997 are now being accepted for the 30th annual award, which will be presented in the summer of 1998. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1997 award, reprints must be received by 1 June 1998.

ANNALS OF THE MISSOURI BOTANICAL GARDEN: CHECKLIST FOR AUTHORS

1. General Instructions

- ☐ Text is in English or Spanish on numbered pages.
- ☐ Manuscript is typed on one side of nonglossy 8½ × 11 in. paper.
- ☐ At least 1 in. is left as margin all around, except on the first page, which has 3 in. left blank at the top.
- ☐ Three copies of double- or triple-spaced printed manuscript, including abstract, legends, tables, specimen lists, Literature Cited, and footnotes, are enclosed.
- ☐ Manuscript is also submitted on MS-DOS/WINDOWS 3½ in. diskette, as WordPerfect® [preferable] file.
- ☐ Right-hand margin is not justified, and words are not broken there.
- ☐ Special typefaces are not used. Common Latin words or phrases are not italicized (e.g., et al., i.e., sensu, etc.).
- ☐ Only names at the rank of genus and below are italicized.
- ☐ Correct accents, umlauts, and other diacritical marks have been included.
- ☐ All figures and tables are cited in the text and are numbered in the order in which they are to appear.
- ☐ Photocopies of the figures are included with each copy of the manuscript.

2. Style

- ☐ Recent issue of the *Annals* is used as a model.
- ☐ *Chicago Manual of Style,* latest edition, is used as a reference.

3. First Page

- ☐ Footnotes are typed as double-spaced paragraphs on the first page. The first footnote contains acknowledgments, including information on granting agencies, herbaria that loaned specimens, and the name of the artist. The second footnote is the author's address. Addresses for additional authors are each separate footnotes. No other footnotes occur, except in tables, where unavoidable.

4. Abstract

- ☐ A one-paragraph abstract precedes text. Papers in Spanish have an English abstract in addition to a Spanish resumen.
- ☐ The abstract is concise (1 paragraph) and includes brief statements about the paper's intent, materials and methods, results, and significance of findings.

5. Tables

- ☐ Tables are neat, double-spaced, and easily understood rather than long and complex.
- ☐ Tables do not contain vertical or horizontal lines. [Editor and/or printer will add them as needed.]
- ☐ Captions are typed double-spaced as paragraphs at the tops of the tables.
- ☐ Each table starts on a separate sheet and is double-spaced.

6. Abbreviations

- ☐ Periods are used after all abbreviations (which are minimized) except metric measures, compass directions, and herbarium designations.
- ☐ When dates are given as part of collection information, three-letter month abbreviations are used, except for months with four letters, which are spelled out in full.
- ☐ States are not abbreviated, and cities are spelled out. [St., as in St. Louis, is acceptable.]
- ☐ Periodicals are abbreviated according to *B-P-H* (*Botanico-Periodicum-Huntianum*) and to *B-P-H/S* (*Botanico-Periodicum-Huntianum/Supplementum*).
- ☐ Authors' names are abbreviated according to Brummit & Powell's *Authors of Plant Names.*
- ☐ Book titles are abbreviated according to *Taxonomic Literature,* edition 2, but with initial letters capitalized. Book titles are spelled out in the Literature Cited.
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- ☐ Species entries are organized as follows: Heading, vernacular name(s), Latin diagnosis (if necessary), description, distribution, summary, specimens examined, discussion. The discussions are parallel and follow the same order, e.g., diagnostic characteristics, distinction from similar species variation, distribution and ecology, nomenclature and typification, uses.
- ☐ One paragraph per basionym is used as follows: *Taxon* author, literature citation, type citation, e.g., *Pleurothyrium amplifolium* (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro: Alto Macahé, *Glaziou 17731* (holotype, B; isotypes, B, G, K, NY, P).
- ☐ Lectotype designations are included together with an indication of where they were designated, the year, and the author. This reference is listed in the Literature Cited. If the author of the paper submitted is making the lectotypification, the phrase "here designated" is used.
- ☐ Exclamation points are used for specimens examined, and types not seen are indicated as such (e.g., MO!, US not seen).
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- ☐ For species with infraspecific taxa: Description and discussion are composite (incorporating all infraspecific taxa) and parallel with other species descriptions. Descriptions of infraspecific taxa are parallel with one another (in the same species). All synonyms are listed under the appropriate infraspecific taxon.
- ☐ Descriptions: Descriptions are parallel, within a given rank. All measurements are metric. Hyphens are used for parenthetical extremes: "peduncle (8.2–)14.3–28.0(–31.9) cm long," unless intermediate values are

not expected: ovary with (2)4(6) locules. Length × width are given in the following manner: lamina 36.4–82.8 × 9.1–16.8 cm.

☐ When relevant, nomina nuda, misapplied names and excluded names are included in the discussion following the description, or at the end of the paper, but are not part of the formal synonymy.

8. Specimens Examined

☐ If many specimens were examined, those cited in the text are limited to ca. 1½ manuscript pages.

☐ An index to specimens examined is placed at the end of the paper, following the Literature Cited. It is arranged alphabetically by collector, followed by collection number, followed by the number of the taxon in the text. Names (including initial(s) of first and second collector are provided, "et al." if three or more.

☐ Specimens are cited in the text as follows: *Additional specimens examined* (or *Selected specimens examined*) MEXICO. **Oaxaca:** Sierra San Pedro Nolesco, Talea, 12°37″N, 85°14′W, 950–1100 m, 3 Feb. 1987 (fl), *Jergensen 865* (BM, G, K, US). [Dates and reproductive status are optional but are omitted from longer lists.] Countries are run together in the same paragraph, e.g., COUNTRY A. **Major political division:** . . . COUNTRY B. **Major political division:** . . . . Separate paragraphs are used for major continental regions within major political divisions.

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☐ If paper presents original data, it includes the citation of herbarium vouchers, as well as vouchers for seed collections, etc. [Depending on the type of paper, reference to the original wild source may also be required.] Vouchers are also cited from common names and uses taken from specimen labels.

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☐ Keys are clear and have been checked carefully for consistency with the descriptions. Leads of each couplet are parallel.

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☐ The Literature Cited contains all references cited in the text.

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CORRESPONDENCE

Amy McPherson,
Managing Editor
Scientific Publications
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299,
U.S.A.

Tel: (314) 577-5112
Fax: (314) 577-9594
Electronic mail:
amcpher@
admin.mobot.org
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Experimental and Molecular Approaches to Plant Biosystematics

The proceedings of the Fifth International Symposium of the International Organization of Plant Biosystematists (IOPB)

Edited by Peter C. Hoch and A. G. Stephenson

Twenty-three original contributions that span the breadth of biosystematics, a dynamic field of study that bridges the realms of systematics and population biology. The papers are arranged in four groups, reflecting the original four symposia of the 1992 meeting. *DNA and Plant Biosystematics* presents innovative work that uses the rapidly developing nucleic acid methods adapted from molecular biology. *Plant Growth Patterns and Biosystematics* includes comparative and developmental analyses of plant architecture and branching patterns. *Plant Reproductive Strategies* surveys new approaches in the analysis of plant reproductive biology, an area central to both systematic and population-level studies. *Phylogenetic Analysis and Population Biology* emphasizes the application of the powerful new methods of phylogenetic analysis to problems at the species and population levels. Monographs in Systematic Botany from the Missouri Botanical Garden, Volume 53. ISBN: 0-915279-30-4. 416 pp. Illustrated. 1995. $60.00 U.S. $62.00 Non-U.S.

Annals of the Missouri Botanical Garden, Volume 82, Number 2: Alternative Genes for Phylogenetic Reconstruction in Plants

A symposium cosponsored by the American Society of Plant Taxonomists and the Botanical Society of America, organized by Pamela S. Soltis and Douglas E. Soltis, and presented at the 1993 AIBS meetings.

Although the chloroplast gene *rbc*L has been successfully used to reconstruct plant phylogeny, many important questions of plant phylogeny and evolution cannot be addressed using it. The contributors to this issue of the *Annals* explore the potential of eight alternative genes or DNA regions for phylogenetic reconstruction at a variety of hierarchical levels. Both nuclear and chloroplast genes are evaluated. Three regions of the nuclear ribosomal RNA cistron are explored: the 18S gene, the internal transcribed spacers (ITS), and the 26S gene. Small multigene families from the nuclear genome may also carry phylogenetic signal: the phytochrome gene family and the small heat shock gene family. Three genes from the chloroplast genome are also considered: *atp*B, *ndh*F, and *mat*K. Each paper describes the location, size, structure, and rate of evolution of the chosen gene and discusses its potential for phylogenetic study. This issue also contains: "The Comparative Pollination and Floral Biology of Baobabs (*Adansonia*–Bombacaceae)" by David A. Baum and "In Memoriam: *Peter G. Martin.*" Annals 82(2) 1995. 174 pages. $27.50 U.S. $28.00 Non-U.S.

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CONTENTS

A Revision of *Styrax* (Styracaceae) for Western Texas, Mexico, and Mesoamerica ..... *Peter W. Fritsch* 705

Systematics of *Kalimeris* (Asteraceae: Astereae) ..... *Hong-ya Gu & Peter C. Hoch* 762

A Review of the Genus *Cydista* (Bignoniaceae) ..... *Warren D. Hauk* 815

Systematics of *Eleusine* Gaertn. (Poaceae: Chloridoideae): Chloroplast DNA and Total Evidence ..... *Khidir W. Hilu & John L. Johnson* 841

The Fruits of *Jasminum mesnyi* (Oleaceae), and the Distinction Between *Jasminum* and *Menodora* ..... *Jens G. Rohwer* 848

Revisión del Género *Galianthe* subg. *Ebelia* stat. nov. (Rubiaceae: Spermacoceae) ..... *Elsa L. Cabral y Nélida M. Bacigalupo* 857

Género *Galianthe* subg. *Ebelia* (Rubiaceae: Spermacoceae): Estudio Palinológico ..... *Stella Maris Pire* 878

The Tanaka-Kaiyong Line—An Important Floristic Line for the Study of the Flora of East Asia ..... *Li Xi-wen & Li Jie* 888

Chromosome Numbers in Compositae, XVII: Senecioneae III ..... *Harold Robinson, Gerald D. Carr, Robert M. King & A. Michael Powell* 893

Book Review. *Guide to the Vascular Plants of Central French Guiana. Part 1* by S. A. Mori et al., reviewed by Paul E. Berry 907

Notice 909

Checklist for Authors 910

Cover illustration. *Eccremocarpus viridis* Ruiz & Pavón, by Phyllis Bick.